

**PREDATION, COMPETITION, AND FACILITATION ON TROPICAL REEFS:  
IMPLICATIONS FOR CORALS AS REEFS DEGRADE**

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IMPLICATIONS FOR CORALS AS REEFS DEGRADE

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## LIST OF ABBREVIATIONS

ANOVA	analysis of variance
approx.	approximately
cm	centimeter
df	degrees of freedom
E	East
g	grams
GLS	generalized least-squares
h	hours
kg	kilograms
LME	linear mixed effects
m	meters
mm	millimeters
MPA	Marine Protected Area
S	South
SD	standard deviation
SE	standard error
spp.	species (plural)
v.	version
vs.	versus

## LIST OF SYMBOLS

#	number
=	equals
>	greater than
$\geq$	greater than or equal to
<	less than
$\leq$	less than or equal to
°	degrees
%	percentage
$\pm$	plus or minus
$\sim$	approximately

## SUMMARY

Tropical coral reefs are among the most diverse and productive ecosystems on Earth, but reefs worldwide have experienced dramatic declines in coral and often transitioned from coral- to macroalgal dominance. As local and global threats to corals increase in severity and frequency, there is an urgent need to understand how reef degradation, as well as efforts to manage and restore corals, are reshaping ecological interactions that are critical to the function of coral reef ecosystems. Here, I utilize a range of experimental approaches to investigate how interactions between corals, competing macroalgae, and coral predators (i.e. corallivores) are being altered within mosaics of coral reef habitat characterized by different levels of degradation and local protection in the tropical Pacific. I first demonstrate, via a series of field observations and experiments, the direct negative effects of competition for corals competing with macroalgae that commonly dominate degraded reefs, including the spatial and temporal constraints of these competitive interactions, as well as the indirect positive effects that can arise due to the presence of a common coral predator, the crown-of-thorns sea star (*Acanthaster cf. planci*). I also provide observational and experimental evidence that protected reefs can help alleviate predation by corallivorous snails (*Coralliophila violacea*) for some stress-tolerant corals (*Porites cylindrica*), but that stark habitat contrasts between coral-dominated protected reefs and macroalgal-dominated fished reefs can simultaneously attract and concentrate feeding by other corallivores (*Acanthaster cf. planci*) – potentially contributing to coral demise and compromising the conservation value of small Marine Protected Areas. Lastly, I use a field-based manipulative experiment to explore the implications of coral species loss for ecosystem function on degraded reefs; demonstrating that greater coral species richness can enhance coral growth and survivorship, and reduced colonization by competing macroalgae. Together, these studies

highlight the need to better understand the novel and context-dependent role of ecological interactions – both for fundamental ecology and effective management – in rapidly changing ecosystems subject to increasing disturbances.

## CHAPTER 1

### SPATIAL AND TEMPORAL LIMITS OF CORAL-MACROALGAL COMPETITION: THE NEGATIVE IMPACTS OF MACROALGAL DENSITY, PROXIMITY, AND DURATION OF CONTACT

#### Abstract

Tropical reefs can experience abrupt and lasting shifts in community composition and ecosystem function when they transition from coral- to macroalgal-dominance. Although negative effects of macroalgae on corals are well documented, whether such effects vary with spatial scale or the density of macroalgae remains inadequately understood, as does the legacy of their impact on coral growth. Using coral- versus macroalgal-dominated areas, we tested effects of macroalgal competition on the Indo-Pacific corals *Acropora millepora* and *Porites cylindrica*. When corals were transplanted to areas of: *i*) macroalgal-dominance, *ii*) macroalgal-dominance but with macroalgae removed, or *iii*) coral-dominance lacking macroalgae, coral growth was equivalently high in plots without macroalgae and low (62-90% less) in plots with macroalgae, regardless of location. In a separate experiment, we raised corals above the benthos in each area and exposed them to differing densities of the dominant macroalga *Sargassum polycystum*. Coral survivorship was high ( $\geq 93\%$  3 months<sup>-1</sup>) and did not differ among treatments, whereas the growth of both coral species decreased as a function of *Sargassum* density. When *Sargassum* was removed after two months, there was no legacy effect of macroalgal density on coral growth over the next seven months; however, there was no compensation for previously depressed growth. In sum, macroalgal impacts were density dependent, occurred only if macroalgae were in close contact, and coral growth was

resilient to prior macroalgal contact. The temporal and spatial constraints of these interactions may have important implications for ecosystem trajectories that lead to reef decline or recovery.

## **Introduction**

Local and global disturbances are negatively impacting foundation species and creating community shifts that reduce ecosystem function and services (Scheffer et al. 2001, Folke et al. 2004). These shifts represent a fundamental change in the structure and function of these systems and are typically characterized by tipping points, feedbacks, and hysteresis (Scheffer et al. 2001). Once established, phase-shifts are difficult to reverse (Scheffer and Carpenter 2003, Folke et al. 2004). Conceptual models suggest that the stability of alternate states arises from interactions among elements of the new state that form feedbacks, reinforcing and maintaining the state (Mumby and Steneck 2008; Hughes et al. 2010). In turn, these feedbacks can lead to hysteresis, where the pathway along which the system may return to its original state differs from the pathway of decline (Scheffer et al. 2001, Mumby et al. 2007). Despite their potential importance, there is a critical gap in our knowledge of feedback mechanisms, how they build or erode the resilience of ecosystems, and the time courses over which they establish or weaken. This understanding is required to predict, avoid, and reverse undesirable phase-shifts.

On tropical reefs, corals provide topographically complex habitat for hundreds of thousands of species (Fisher et al. 2015) and economic goods and services for millions of people (Moberg and Folke 1999). However, recent natural and human-induced stressors (Harvell et al. 2007, Hoegh-Guldberg et al. 2007, Hughes et al. 2017) have decimated these foundation species, with many reefs transitioning to structurally simplified systems



with low coral cover and increased cover of macroalgae that compete with corals (Mumby and Steneck 2008, Hughes et al. 2010). As competitive interactions between corals and macroalgae increase, macroalgae are expected to hasten coral decline, limit coral recovery (Mumby and Steneck 2008, Hughes et al. 2010), and enhance macroalgal resilience via positive feedbacks (Hoey and Bellwood 2011, Dell et al. 2016, van de Leemput 2016). Macroalgae can directly harm corals via physical mechanisms such as shading, abrasion, and overgrowth (McCook et al. 2001), chemical mechanisms such as allelopathy (Rasher et al. 2011, Vieira et al. 2016), suppression of coral recruitment (Kuffner et al. 2006, Paul et al. 2011, Dixon et al. 2014), or releasing water-soluble compounds (Haas et al. 2011, Jorissen et al. 2016) that may disrupt coral microbiomes and stimulate coral pathogens (Nugues et al. 2004, Smith et al. 2006, Barott et al. 2012). Macroalgae also alter coral interactions with corallivores (Wolf and Nugues 2013, Clements and Hay 2015, Brooker et al. 2016).

Despite evidence that macroalgal competition harms corals (McCook et al. 2001, Birrell et al. 2008), there are few field-based manipulative experiments investigating the long-term consequences of macroalgal competition for coral fitness (e.g., River and Edmunds 2003, Box and Mumby 2007, Hughes et al. 2007, Ferrari et al. 2012a). Especially lacking are investigations of how the density of macroalgae, and the proximity to natural, multispecies assemblages of macroalgae common to degraded reefs affect corals. Studies to date have focused primarily on the impacts of an individual macroalga on an individual coral, rather than how impacts vary with macroalgal density or when contacting single species (experimentally) versus the multispecies assemblages that occur in the field.

We conducted manipulative field experiments to investigate the long-term effects of macroalgal competition on growth and survivorship of the corals *Acropora millepora* and *Porites cylindrica*, both common to Indo-Pacific reefs. We used a coral-dominated no-take Marine Protected Area (MPA) and adjacent macroalgal-dominated fished area to investigate: 1) the long-term effects of differing macroalgal cover on coral survivorship and growth, 2) whether a history of macroalgal presence altered coral resistance or resilience to competition, 3) the effects of algal density of coral growth and survivorship, and 4) the resilience of coral growth following algal removal.

## **Materials and Methods**

### ***Study site and organisms***

This study was conducted within neighboring sections of shallow (1.5–2.5 m deep) lagoonal back reefs that were either coral-dominated (a no-take MPA) or macroalgal-dominated (a fished area) at Votua Village along the Coral Coast of Viti Levu, Fiji (18° 13.05'S, 177°42.97'E). Both areas are similar in depth and physical regimes, but differ in reef community assemblages, which diverged from a similar benthic state across the entire area when the MPA was established about ~11 years before our experiment (Simpson 2010). Within the MPA, corals are now abundant (~55% cover) and macroalgae rare (< 3%) on hard substrates, while the fished area supports few corals (~4% cover), few herbivorous fishes, and high cover of macroalgae (~91%; Rasher et al. 2013).

Our study consisted of two field-based manipulative experiments assessing the long-term (3-9 month duration) effects of macroalgae on coral growth and survivorship. In each case, we used the corals *Acropora millepora* and *Porites cylindrica* (hereafter

*Acropora* and *Porites*), which are common on reefs throughout the Indo-Pacific and are representative of coral families differing in growth rates (Darling et al. 2012) and tolerances to various stressors (e.g., macroalgal allelopathy, *Acanthaster* spp. predation, bleaching; Pratchett 2007, Rasher et al. 2011, Bonaldo and Hay 2014).

***Influence of proximity to natural macroalgal assemblages on coral growth and survival***

To determine the effect of natural macroalgal assemblages and environmental legacy effects on coral growth and survivorship, we conducted a reciprocal transplant experiment using corals from the macroalgal- versus coral-dominated areas. Corals collected from each area were reciprocally transplanted to benthic plots (0.5 x 0.5 m) in each area where macroalgae were either (i) naturally present (macroalgal-dominated area), (ii) routinely removed at ~3-week intervals (macroalgal-dominated area) or (iii) naturally absent (coral-dominated area). In December 2013, five branches (6-8 cm in length) were collected from each of 20 colonies of *Acropora* and *Porites* within the coral-dominated MPA and macroalgal-dominated fished area at Votua Reef (100 branches species<sup>-1</sup> area<sup>-1</sup>). Individual branches were affixed into the cut-off necks of inverted plastic bottles using epoxy (Emerkit) and the screw-off top of bottles was secured, inverted, to the substrate with a nail. This procedure allowed us to easily transplant individuals to our benthic plots and to detach and reattach them for periodic weighing with minimal disturbance. Corals were initially interspersed on galvanized metal racks (~1.5 m water depth, and 0.75 m above the substratum) in their area of origin for ~1-month to allow acclimation and recovery from fragmentation. During this time, we established a series of twenty benthic plots for each of the three treatments (i.e.,

macroalgae present, macroalgae removed, macroalgae naturally absent), each of which were interspersed haphazardly within a ~100 m stretch of reef at ~1.5 m depth and marked with flagging tape. Adjacent plots were separated by a minimum of ~4 m. Following the recovery period, one branch from each colony of each species (*Acropora* and *Porites*) and each area (coral- and macroalgal-dominated) was haphazardly selected and allocated to a plot within each treatment (4 branches plot<sup>-1</sup> treatment<sup>-1</sup>). Corals were screwed into one of four bottle caps haphazardly embedded within the benthos near the center of their designated plot. Bottle caps, and hence corals, within each plot were separated by ~15-20 cm. This reciprocal transplantation allowed us to compare whether corals responded differently when grown in plots without macroalgae in the coral- and macroalgal-dominated areas, and whether a coral's environmental legacy (i.e., originating in the coral- or macroalgal-dominated area) influenced its performance in different plots and/or areas.

Coral growth and survivorship were monitored at five intervals over the 36 weeks between 22 January and 4 October 2014. Corals were 'unscrewed' from the substratum and weighed in the field using an electronic scale (OHAUS Scout Pro) enclosed within a plastic container that was mounted to a tripod holding it above the water surface. Twenty-four to 48 hours before weighing sessions, each coral's bottle-top/epoxy base was lightly brushed to remove fouling organisms. During weighing sessions, each coral was gently shaken 30 times to remove excess water, weighed, and then immediately placed back into the water and reattached to the substrate. At the end of the experiment, corals were separated from their epoxy base and each coral and base weighed separately. This allowed the relative change in coral mass (as a percentage of initial mass) to be

determined for each sampling period.

Differences in growth (% change in mass) among surviving conspecifics of different locations (macroalgal- versus coral-dominated area), plots (macroalgae present versus absent), and origins (macroalgal- versus coral-dominated area) were assessed using the “compareGrowthCurves” function in the R (version 3.3.2) package “statmod” (<http://bioinf.wehi.edu.au/software/compareCurves/>). *P*-values were adjusted for multiple pairwise comparisons using Hommel’s method. Differences in total mortality among conspecifics of different locations, plots, and origins were compared using Fisher’s exact tests, with *p*-values adjusted for multiple contrasts using the Bonferroni method.

During each assessment of coral mass, we simultaneously surveyed the percent cover and canopy height of macroalgae immediately surrounding corals within plots where macroalgae were not removed to document changes in the benthic community that might affect coral growth, such as seasonal changes in abundance of macroalgal species like *Sargassum* that dominate the fished area (Rasher et al. 2013, Dell et al. 2016). A 25 x 25 cm quadrat divided into 25 equal (i.e., 5 x 5 cm) subsections was centered over each coral’s attachment site, and percent cover of the dominant organisms/substrate types (e.g., macroalgae [to genus], live coral, dead coral, rubble, sand, etc.) within each 5 x 5 cm grid was estimated visually. Temporal differences in macroalgal cover within our plots were analyzed using a linear mixed effects (LME) model in R (v. 3.3.2) (R Core Team 2016) using the package nlme (Pinheiro et al. 2017). Models were fitted using restricted maximum likelihood with time (week) as a fixed factor and individual replicate quadrats from each plot as a random factor to account for spatial and temporal non-independence between samples. To control for heteroscedasticity, we modeled within-

group error for each time point using the varIdent argument. Multiple comparisons of means were performed using generalized linear hypothesis test (glht) and Tukey's (HSD) test in the multcomp package (Hothorn et al. 2008). We also estimated the maximum and average height of the macroalgal canopy above the benthos within each quadrat by measuring the height of the tallest macroalga and the height of the canopy at five random points, respectively, within each quadrat using a ruler. Both maximum and average height data were then used to obtain a maximum and mean overall canopy height for macroalgae in each plot ( $n = 20$  plots treatment<sup>-1</sup>). Temporal differences in maximum and average canopy heights were analyzed separately with a one-way repeated measures ANOVA followed by Tukey post hoc tests using JMP (v. 13.0.0).

### ***Influence of Sargassum density on coral growth***

To investigate the effect of macroalgal density on the growth and survivorship of corals, we exposed branches of *Acropora* and *Porites* to different densities of *Sargassum polycystum* for 2 months. *Sargassum* is a canopy-forming macroalga that dominated macroalgal assemblages (71-94%) in our benthic plots and is abundant on degraded reefs in Fiji and worldwide (e.g., Hughes 1994, Ledlie et al. 2007, Rasher et al. 2013, Chong-Seng et al. 2014). To create standardized units of *Sargassum*-coral contact, 6-8 cm length branches of *Acropora* and *Porites* corals were collected from colonies within both the macroalgal- and coral-dominated areas of Votua Reef (15 colonies species<sup>-1</sup> area<sup>-1</sup>) and individually epoxied into the cut-off necks of inverted plastic bottles during November 2013 (as described above). Each coral and its epoxy/bottle-top base was then screwed into a bottle cap embedded within a cement cone and interspersed on one of four galvanized metal racks (Figure 1.1), positioned so that rack tops were about 50 cm above

the reef substratum and at ~1 m depth during low tide. Racks were located in the area where the coral was collected (i.e., transplants were not reciprocal), but were elevated above the reef substrata to isolate corals from confounding factors associated with the benthos (e.g., sand scour, benthic predators). Corals were allowed to acclimate for ~1 month, after which they were exposed to one of four algal treatments.

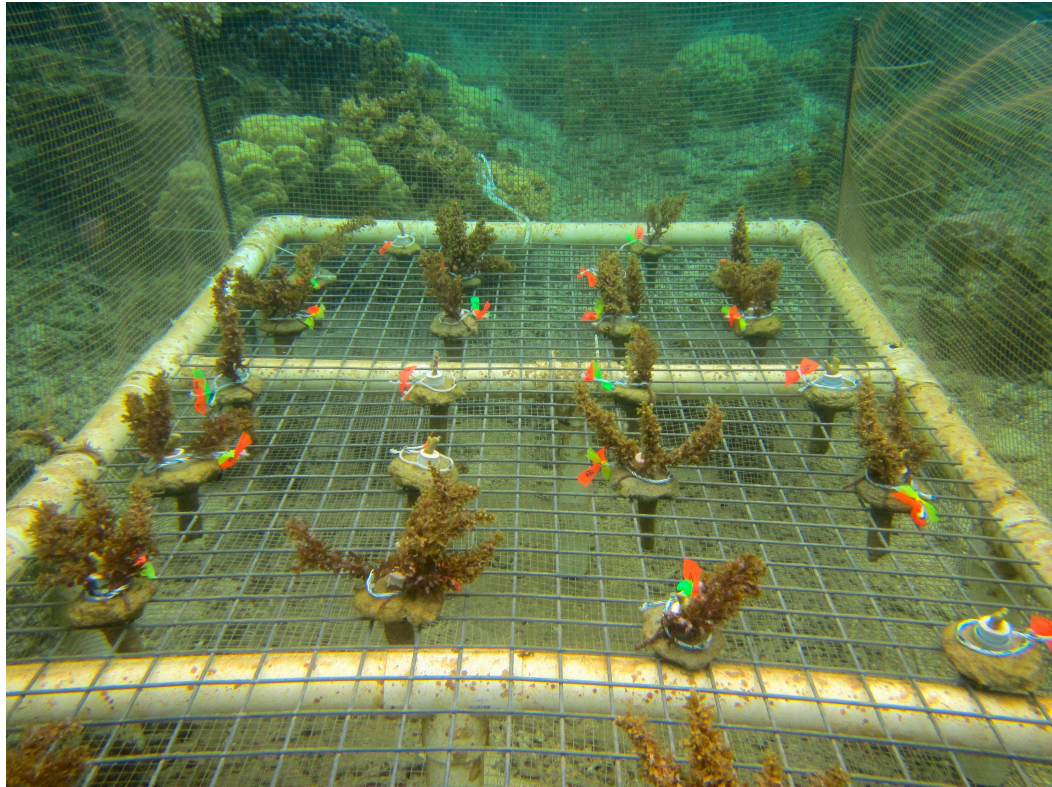


Figure 1.1: Experimental design used for coral-macroalgal pairs in the coral growth experiment conducted on elevated metal racks.

In December 2013, whole *Sargassum* thalli (length = 15-20 cm) were collected from the macroalgal-dominated area and either 0, 1, 3, or 6 thalli were inserted into a three-stranded rope (length = 18-20 cm) that was slipped over two 4 cm nails embedded 180° apart on the upper surface of the cement cone (following Rasher and Hay 2010). The base of each *Sargassum* thallus was held 2-4cm from the coral, such that the thallus was lightly contacting the experimental corals. All racks were caged with 1 cm<sup>2</sup>-grid galvanized metal mesh to exclude large herbivorous fishes, and all cages were brushed weekly to remove fouling organisms. During weekly maintenance, any *Sargassum* displaced from the ropes (e.g., because of wave action) was replaced. *Sargassum* density treatments were applied to corals for three months (December 19-20, 2013 to March 15-16, 2014), and the mass of corals (including their epoxy/bottle-top base) were assessed after two (February 13-14) and three months of contact. At the end of this three-month period, all algae were removed (as was the mesh caging), and the corals were maintained for a further six months to evaluate any legacy effects of past macroalgal contact. After six months of no macroalgal contact, each coral was separated from its base, and the bases and corals were weighed separately to allow relative growth rates to be calculated.

To compare the effects of *Sargassum* density and coral origin (coral- and macroalgal-dominated area) on coral growth, differences in relative growth (as percentage of initial weight) at three months (the algal density treatment) and nine months (six months following algal removal), as well as the total change in mass (g) for *Acropora* and *Porites* during the entire nine-month experiment, were analyzed using generalized least square (GLS) models in R (v. 3.3.2) (R Core Team 2016) with the package nlme (Pinheiro et al. 2017). In each case, we used model selection to



sequentially test nested GLS models via likelihood ratio tests to obtain the optimal fixed structure for each model (following Zuur et al. 2009). When necessary, the varIdent argument was used to control for heteroscedasticity. Following model selection, the significance of remaining fixed terms was tested using likelihood ratio tests. Subsequent multiple comparisons of means were performed using the generalized linear hypothesis test (glht) and Tukey (HSD) test in the multcomp package (Hothorn et al. 2008).

## Results

### *Coral growth and survival in plots with versus without natural macroalgal assemblages*

When transplanted to benthic plots, surviving *Acropora* increased in mass ~11.3-14.5x from their initial mass over the 36-week period if they were not surrounded ( $\leq 50$  cm) by macroalgae (i.e., macroalgae removed and macroalgae absent plots). By contrast, *Acropora* surrounded by natural macroalgal assemblages increased in mass by only ~3.9-4.9x (a 57-72% reduction in growth). These patterns were unaffected by coral origin or location to which they were transplanted, so long as macroalgae had been removed within 50 cm of the transplants (Figure 1.2A). Similarly, surviving *Porites* in plots without macroalgae increased in mass ~4.0-7.0x, while those surrounded by macroalgae increased only ~1.6-1.9x (a 52-77% reduction; Figure 1.2B). Interestingly, *Porites* from the macroalgal-dominated area that were transplanted to the coral-dominated area exhibited 1.6-2x greater growth than *Porites* in areas cleared of macroalgae or *Porites* collected from, and transplanted to, the coral-dominated area (Figure 1.2B).

After 36 weeks, the mortality of *Acropora* (45-75%, 9-15 of 20 individuals per treatment) was greater than that of *Porites* (10-25%, 2-5 of 20;  $p < 0.001$ ; Fisher Exact test), but did not differ among treatments for either species (*Acropora*:  $p = 1.000-0.105$ ,

*Porites*:  $p = 1.000-0.408$ , Fisher Exact tests; Figure 1.2C & D).

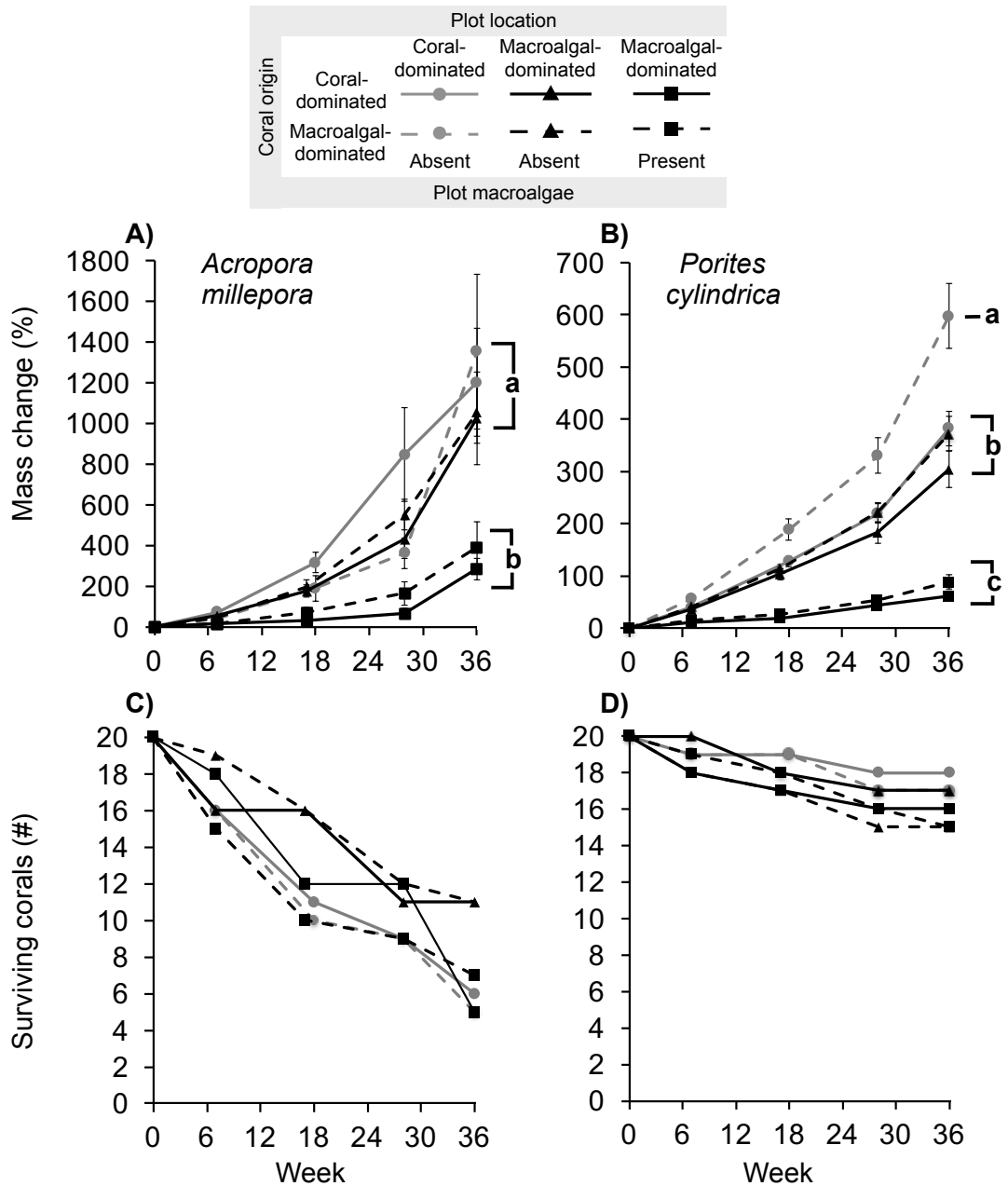


Figure 1.2: (Top) Percentage change in coral mass (mean  $\pm$  SE) during a 36-week period (January-October 2014) for *Acropora millepora* (A) and *Porites cylindrica* (B) originally from the coral- or macroalgal-dominated area that were embedded within coral- or macroalgal-dominated area plots (with natural algal assemblages either left in place or physically removed within the fished area location). Growth differences among conspecifics were analyzed using the “compareGrowthCurves” function in the R package “statmod.” Letters to the right of lines indicate significant groupings via Hommel’s

method ( $p < 0.05$ ). (Bottom) The number of *Acropora* (C) and *Porites* (D) that survived throughout the duration of the experiment. Survival did not differ as a function of treatment for either species.

During our experiment, percent cover of macroalgae surrounding corals in the macroalgal-dominated area where we did not remove macroalgae ranged from 81-97%, with *Sargassum* accounting for ~71-94% of total cover (Figure 1.3). Macroalgal cover and canopy height were greatest when sampled in the Austral summer (January and March) and lowest during the Austral winter (May and August) (Figure 1.3). Macroalgal cover or height in the coral-dominated area or in our removal treatments was not measured because it was always minimal - we visually estimated cover and height in these areas as below 1% and 0.5 cm, respectively.

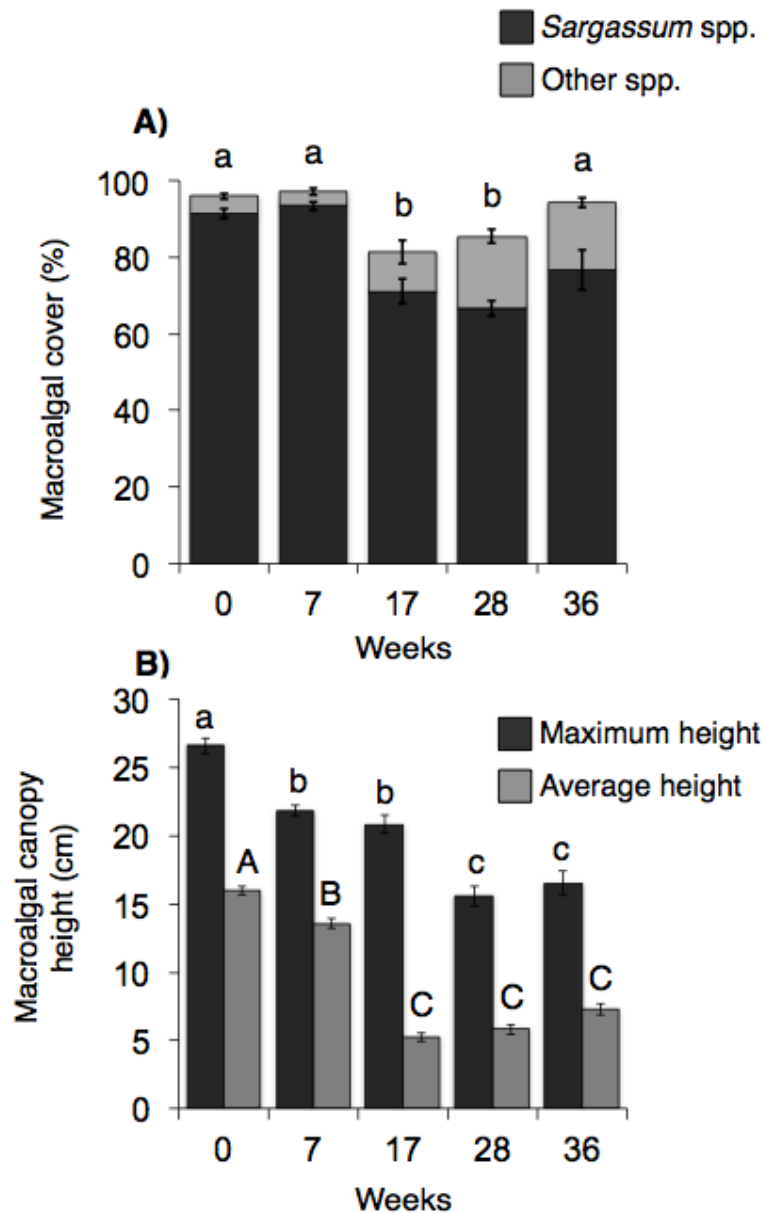


Figure 1.3: A) Algal percent cover, January-October 2014, within plots in the macroalgal-dominated area where natural macroalgal assemblages were present. Temporal differences in percent macroalgal cover were analyzed using a linear mixed effect model ( $p < 0.001$ ) and letters denote significant differences ( $p < 0.05$ ) among times via Tukey tests. B) Maximum (black bars) and average (gray) macroalgal canopy height in plots with macroalgae during January-October 2014. One way repeated measures ANOVA were used to analyze temporal differences in maximum canopy height ( $F_{(4,73)} =$

30.76,  $p < 0.001$ ) and average canopy height ( $F_{(4,72)} = 93.04$ ,  $p < 0.001$ ). Letters denote significant differences ( $p < 0.05$ ) among months via Tukey tests.

### ***Influence of Sargassum density on coral growth***

When surrounded by *Sargassum* on experimental racks, growth of *Acropora* and *Porites* strongly decreased with increasing *Sargassum* density ( $p < 0.001$ ; Figure 1.4A & B); effects did not vary by coral origin ( $L = 0.449$ ,  $p = 0.503$  for *Acropora*,  $L = 3.661$ ,  $p = 0.056$  for *Porites*). The presence of a single *Sargassum* thalli reduced *Acropora* growth by ~48% compared to *Acropora* without macroalgae (Figure 1.4A). Increasing the density of *Sargassum* by 3- and 6-fold (i.e., three and six thalli) reduced growth by a further ~15% in each case (Figure 1.4A). Growth of *Porites* adjacent to one *Sargassum* thalli was reduced by ~29% compared to *Porites* without *Sargassum*, while 3- and 6-fold increases in the density of *Sargassum* reduced growth by ~16 and 27%, respectively (Figure 1.4B). Survivorship was high for both species; only 5% of *Acropora* and 2% of *Porites* died during this three-month period (Figure 1.4A & B).

Six months after the removal of the *Sargassum* treatments, the absolute growth (g increase) of each species was still depressed as a function of past *Sargassum* density ( $p < 0.001$ ; Figure 1.4E & F), but did not vary by coral origin ( $L = 0.282$ ,  $p = 0.595$  for *Acropora*,  $L = 0.146$ ,  $p = 0.702$  for *Porites*), thus resembling patterns established during the first three months when *Sargassum* was present. However, once the size of the corals at three months was taken into account, the relative growth rates (% growth) after *Sargassum* was removed did not differ as a function of previous *Sargassum* density ( $L = 0.844$ ,  $p = 0.839$  for *Acropora*,  $L = 7.650$ ,  $p = 0.054$  for *Porites*; Figure 1.4C & D) or coral origin ( $L = 1.171$ ,  $p = 0.279$  for *Acropora*,  $L = 0.759$ ,  $p = 0.384$  for *Porites*).

Eighty-nine percent of *Acropora* and 97% of *Porites* on the racks survived through the

entire experimental period (Figure 1.4E & F); this was considerably greater than the 25-55% survival of *Acropora* and the 75-90% survival of *Porites* on the natural substrate over this time period (Figure 1.4C & D).

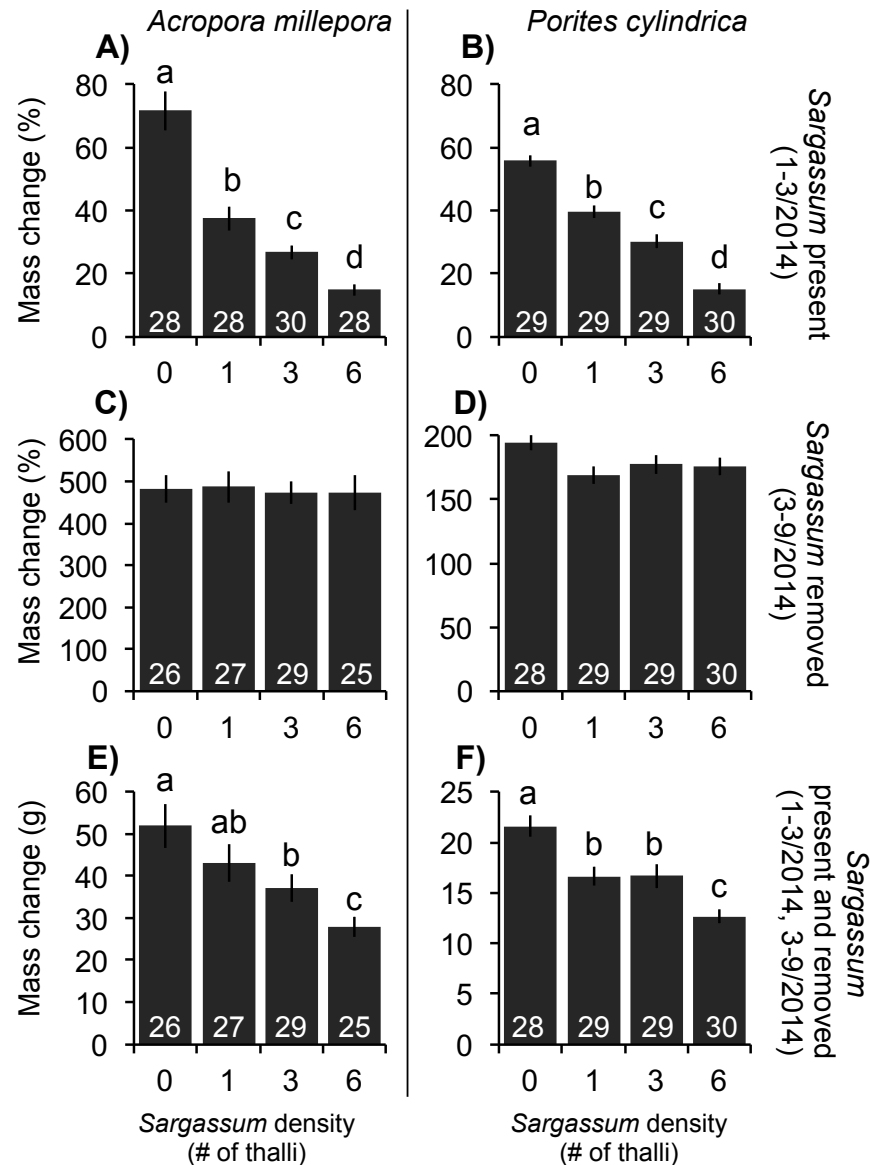


Figure 1.4: (Top) Percentage change in mass (mean  $\pm$  SE) for the corals *Acropora millepora* (A) and *Porites cylindrica* (B) over two months (January–March 2014) of contact with differing densities of *Sargassum polycystum*. (Middle) Percentage change in mass (mean  $\pm$  SE) during March–September 2014 for *Acropora* (C) and *Porites* (D) previously exposed to different densities of surrounding *Sargassum*, but with no

*Sargassum* present during this period of growth assessment. (Bottom) Total mass change (g) (mean  $\pm$  SE) during January–September 2014 for *Acropora* (E) and *Porites* (F) initially exposed to different densities of *Sargassum* for three months (December–March 2014), but with *Sargassum* then removed and absent for the next 7 months (March–September 2014). For all graphs, data for each species were analyzed using generalized least-squares (GLS) models. Letters denote significant differences ( $p < 0.05$ ) among months via Tukey tests. Numbers within bars indicate sample size.

## Discussion

Resolving the temporal and spatial scales at which macroalgae can negatively impact corals is critical for predicting, avoiding, and reversing phase-shifts on reefs (Mumby and Steneck 2008, Hughes et al. 2010, Graham et al. 2013). We found (1) macroalgae had a dramatic effect on coral growth, irrespective of previous macroalgal exposure or whether corals were located within coral- or macroalgal-dominated reefs, (2) negative effects on coral growth increased with increasing macroalgal density, and (3) these effects were broadly consistent for taxonomically-disparate corals; however, (4) negative growth effects were eliminated if macroalgae were  $\geq 50$  cm away, and (5) the rate at which macroalgal effects on corals commence or cease were immediate. Together, these findings have implications for understanding the spatial and temporal scales at which feedbacks form and are broken.

Reefs may “flip” from coral- to macroalgal-dominance and not return to their coral-dominated state due to alterations in the growth, mortality, and/or recruitment of corals, or a range of other processes (Mumby and Steneck 2008, Graham et al. 2015). Although we found coral growth to be suppressed by the presence and density of macroalgae, there were no legacy effects of prior macroalgal exposure on future coral growth. Our results show that the growth of corals within a degraded system can rapidly recover if close-proximity macroalgae are removed. Following three months of contact by differing densities of *Sargassum*, all corals on our experimental racks immediately

recovered ‘normal’ growth rates upon *Sargassum* removal, suggesting that macroalgae did not produce a persistent negative feedback on coral growth following removal. We also found no negative effects of growing within a macroalgal-dominated habitat, as might be expected if macroalgal release of DOC was affecting the general area by suppressing coral health via alterations of coral microbiomes or other critical processes (Barott and Rohwer 2012, Morrow et al. 2013). Both previous investigations finding that macroalgal dominance did not enhance reef-scale DOC concentrations (Dinsdale et al. 2008, Nelson et al. 2011) and our data suggest that if water-soluble macroalgal exudates are affecting corals, then impacts will be very localized, operating at scales of centimeters or less near the coral-macroalgal interface (Smith et al. 2006, Morrow et al. 2013, Jorissen et al. 2016).

We did not investigate the specific mechanisms by which close-proximity macroalgae reduced coral growth, but these may include a variety of physical (e.g., shading, abrasion, increased sedimentation) or small-scale (mm-cm) chemical or microbially mediated effects (McCook et al. 2001, Rasher et al. 2011, Vieira et al. 2016, Zaneveld et al. 2016). Interestingly, the relationship between coral growth and *Sargassum* density appeared curve-linear, with the greatest reductions in growth realized following the addition of a single *Sargassum* thallus. Further increases in the density of *Sargassum* led to smaller reductions in coral growth. Such relationships may provide some insights into the underlying mechanisms, however, the limited number of densities examined preclude generalizations, and one previous study demonstrated a more linear decrease in the growth of *Montipora* corals with increasing macroalgal density (Clements and Hay 2015). Further experiments will be necessary to determine whether our findings are



broadly applicable to interactions between other species of coral and macroalgae, as well as whether algal effects vary with interaction duration and/or in combination with other stressors (Zaneveld et al. 2016).

While the presence or absence of macroalgae strongly influenced coral growth, survivorship was statistically indistinguishable for conspecific corals in our benthic plots whether macroalgae was present or absent. Corals elevated off of the benthos also exhibited comparable survivorship when surrounded by multiple densities of *Sargassum*, suggesting that competition with *Sargassum* may be costly for corals in terms of growth, but rarely results in whole colony mortality over the time periods we investigated. In contrast, other macroalgal species that are strongly allelopathic can cause mortality for some corals (including *Acropora millepora*) over periods of only days to two or three weeks (Rasher et al. 2011). Other benthic disturbances, such as sand scouring, damage from dislodged coral heads during storms, and/or crown-of-thorns sea star predation were observed in several instances (C. Clements, personal observation) and may have contributed to coral mortality on the natural benthos. Reef decline is commonly characterized by punctuated disturbance events (e.g., hurricanes, crown-of-thorns outbreaks, bleaching events) that reduce coral cover, followed by periods of relative stasis rather than coral recovery (Hughes 1994, Gardner et al. 2003, Graham et al. 2015). Our findings suggest that macroalgal competition may limit the re-growth of established corals and growth of new corals, and may also impose opportunity costs associated with delayed growth (e.g., increased mortality risk, and decreased competitive ability and fecundity; Hall and Hughes 1996, Zilberberg and Edmunds 2001, Edmunds and Gates 2004). Therefore, even low densities of macroalgae could inhibit recovery of corals

between disturbance events; contributing to the “ratcheting down” of coral reef ecosystems. However, if natural processes (e.g., herbivory, seasonality; Ferrari et al. 2012b, Duran et al. 2016) keep macroalgae in check, it appears that remaining corals should be able to rapidly recover their growth potential.

Other studies have documented evidence that canopy-forming macroalgae like *Sargassum* experience enhanced growth (Dell et al. 2016) and reduced herbivory (Hoey and Bellwood 2011, Dell et al. 2016) when growing in dense stands – constituting positive feedbacks that reinforce *Sargassum* dominance. Our data demonstrate that the density of *Sargassum* also impacts coral growth, which may increase *Sargassum*’s ability to monopolize space and further reinforce *Sargassum* dominance. Conversely, reductions in the density of *Sargassum* may promote proportional increases in growth and recovery of existing corals; increasing reef structural complexity and recruitment of herbivorous fishes (Mumby and Steneck 2008, Graham and Nash 2013) that could undermine *Sargassum* dominance (Hoey and Bellwood 2011; Rasher et al. 2013). Targeted reductions of direct interactions between macroalgae and corals may also help promote coral growth, recovery, and reproductive potential of corals currently inhabiting macroalgal-dominated reefs (Graham et al. 2013).

Our study highlights the negative impacts of macroalgae that are common to degraded reefs. However, our data also demonstrate that some corals may be resilient to macroalgal competition depending on the temporal and spatial scales of these interactions and how they impact trajectories of benthic community structure on disturbed reefs. Our findings dovetail with evidence from previous studies, suggesting that preserving or restoring critical ecosystem processes such as herbivory can limit macroalgae and lead to

enhanced coral persistence and recovery (Mumby and Harborne 2010, Gilmour et al. 2013). Understanding the context-dependencies inherent to common coral-algal interactions will be particularly important as global-scale disturbances continue to challenge management and conservation of vulnerable coral reef ecosystems.

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## CHAPTER 2

### COMPETITORS AS ACCOMPLICES: SEAWEED COMPETITORS HIDE CORAL FROM PREDATORY SEA STARS

#### Abstract

Indirect biotic effects arising from multispecies interactions can alter the structure and function of ecological communities – often in surprising ways that can vary in direction and magnitude. On Pacific coral reefs, predation by the crown-of-thorns sea star, *Acanthaster planci*, is associated with broad-scale losses of coral cover and increases of macroalgal cover. Macroalgal blooms increase coral-macroalgal competition and can generate further coral decline. However, using a combination of manipulative field experiments and observations, we demonstrate that macroalgae, such as *Sargassum polycystum*, produce associational refuges for corals and dramatically reduce their consumption by *Acanthaster*. Thus, as *Acanthaster* densities increase, macroalgae can become coral mutualists, despite being competitors that significantly suppress coral growth. Field feeding experiments revealed that the protective effects of macroalgae were strong enough to cause *Acanthaster* to consume low preference corals instead of high preference corals surrounded by macroalgae. This highlights the context-dependent nature of coral-algal interactions when consumers are common. Macroalgal creation of associational refuges from *Acanthaster* predation may have important implications for the structure, function and resilience of reef communities subject to an increasing number of biotic disturbances.

## **Introduction**

Indirect biotic interactions can strongly impact the structure and function of ecological communities, but the mechanisms and circumstances controlling their relative importance is incompletely understood (Strauss 1991, Wootton 1994, Menge 1995, Berlow 1999). Indirect biotic effects occur when the impact of one species on another is mediated by the presence of a third (Wootton 1994). This commonly entails modifying the density (i.e. density-mediated indirect interactions) or traits (e.g. behaviour, morphology, life history) of one species, which goes on to influence subsequent interactions among other species (Werner and Peacor 2003, Preisser et al. 2005, Ohgushi et al. 2012). These effects are ubiquitous across ecological systems and are known to influence a myriad of species interactions (e.g. competition, predation, mutualism), as well as community- and ecosystem-level processes (Pace et al. 1999, Werner and Peacor 2003, Schmitz et al. 2004, Long and Hay 2012). A substantial body of work has highlighted the role of indirect effects in competitive interactions between species, including situations in which the strength or qualitative sign of competitive effects on one species can be altered when its competitor ameliorates the negative impacts of an extrinsic stressor, such as predation by a third species (i.e. ‘associational refuge’) (Atsatt and Odowd 1976, Hay 1986, Bruno et al. 2003). A better understanding of context-dependency is needed for both modelling indirect interactions and for building robust management strategies for ecosystems subject to increasing disturbances (Bruno et al. 2003, He et al. 2013).

Coral reefs provide a good example of the needs for, and values of, understanding indirect interactions. Reefs are in worldwide decline because of a variety of natural and

anthropogenic disturbances (Gardner et al. 2003, Bellwood et al. 2004, Bruno and Selig 2007, Hughes et al. 2010), with declines in coral cover commonly accompanied by increases in benthic macroalgae (Hughes 1994, Mumby and Steneck 2008, Hughes et al. 2010). Macroalgae use a variety of physical (e.g. shading, abrasion, overgrowth) and/or chemical (i.e. allelopathy) mechanisms to directly reduce coral recruitment, growth, survival and fecundity (McCook et al. 2001, Birrell et al. 2008, Rasher et al. 2011, Rasher and Hay 2014). Coral-algal interactions may also suppress corals indirectly by promoting virulent bacteria (Smith et al. 2006b, Barott et al. 2012), or by stressing corals in ways that attract corallivores that further damage competing corals (Wolf and Nugues 2013). Alternatively, despite being competitors, seaweeds may hide susceptible corals from fish consumers (Venera-Ponton et al. 2011, Bulleri et al. 2013) or buffer stressful physical conditions (Jompa and McCook 1998). The direct and indirect effects of macroalgae on corals, coupled with the increasing prevalence of macroalgal-coral competition, may impact the current and future function of coral reef ecosystems, but the relative cost versus possible benefits of macroalgae to corals remains poorly understood, as does how this may vary as a function of local biotic context (Jompa and McCook 1998, Hughes et al. 2010, Venera-Ponton et al. 2011, Bulleri et al. 2013, Wolf and Nugues 2013).

On Pacific coral reefs, coral consumption by the crown-of-thorns sea star, *Acanthaster planci*, is a major driver of coral loss (Bruno and Selig 2007, De'ath et al. 2012). During *Acanthaster* outbreaks, reef corals can be devastated over large areas, resulting in cascading losses of other species, and decline of reef resilience and function (Moran 1986, Kayal et al. 2012b). If macroalgal competitors sheltered corals from

*Acanthaster* predation, they could have a net positive impact on corals despite being important competitors. Such an associational refuge could alter *Acanthaster* feeding preferences, with implications for reef community composition and local persistence of coral species favoured by *Acanthaster*. Assessing the context-dependent nature of these interactions requires a greater understanding of the relative costs (e.g. competition) versus benefits (e.g. potential associational refuge) for corals in contact with benthic macroalgae.

Here we explored the direct negative and indirect positive effects arising from competitive interactions between corals and macroalgae. Using a combination of manipulative and observational field experiments, we investigated the effects of a common brown macroalga, *Sargassum polycystum*, on the coral *Montipora hispida*, and how costs and benefits for the coral may vary because of *Acanthaster* feeding and *Sargassum* abundance. *Sargassum* is a canopy-forming macroalga that blooms on degraded reefs worldwide (Lewis 1986, Hughes et al. 2007, Rasher et al. 2013), while *Montipora* is a common coral that frequently contacts *Sargassum* on overfished or degraded reefs (Bonaldo and Hay 2014). *Montipora* is also a favoured prey of *Acanthaster*, which is common on both healthy and degraded reefs in Fiji (Zann et al. 1987, Dulvy et al. 2004), and is regularly observed feeding on *Montipora* (C. Clements, personal observation). We hypothesized that at sufficient densities, *Sargassum* not only would reduce coral growth, but also might provide *Montipora* with an associational refuge from *Acanthaster*. For the latter, this included testing whether the probability of *Acanthaster* attacking *Montipora* declined with *Sargassum* density, as well as whether the preference of *Acanthaster* for *Montipora* over *Porites cylindrica* (a low-preference

prey) would reverse if *Montipora* was competing with high densities of *Sargassum*.

## **Material and Methods**

### ***Study site***

This study was conducted within a no-take Marine Protected Area paired with an adjacent fished area on the reef flat (1.5-2.5 m deep) at Votua Village along the Coral Coast of Viti Levu, Fiji (188813.049°S, 1778842.968° E). All manipulative experiments were conducted within the reserve, where corals on hard substrates were abundant (approx. 55% cover) and macroalgae were uncommon (approx. 2% cover), while the field survey of *Acanthaster* feeding on corals as a function of natural macroalgal cover was conducted in the fished area where macroalgae were abundant (91%) and corals were uncommon (approx. 5% cover) (Rasher et al. 2013).

### ***Influence of Sargassum on Montipora growth***

We conducted a manipulative experiment within Votua's no-take reserve during December 2013-March 2014 to test whether prolonged contact with *Sargassum* affects *Montipora* growth rates, and whether these effects vary with the density of surrounding *Sargassum*. We collected five branches of *Montipora* of similar size (approx. 3.5-4.5 g) from each of 20 colonies (100 branches total) located on the reef flat of the reserve and attached them individually to cut-off necks of inverted plastic bottles using epoxy (Emerkit). Each bottle portion and respective coral was then screwed individually into a bottle cap embedded within the substrate. The five *Montipora* branches collected from each colony were then surrounded by one of five algal treatments: 0, 2, 4, 6 or 8 fronds of the brown alga *S. polycystum* (length = 15-20 cm; n = 20 per treatment; Figure 2.1). All *Sargassum* was collected from the adjacent fished area. To manipulate coral-algal

contact, two 5 cm nails were embedded into the substrate on opposite sides of the bottle cap so that a three-stranded rope could be slipped over the nail head to hold the seaweed in contact with the coral. All corals and surrounding macroalgae were caged with 1 cm<sup>2</sup>-grid metal screening to exclude herbivorous fishes, and all cages were brushed at least once every 9 days to remove fouling organisms. During routine maintenance, any *Sargassum* displaced from the ropes (e.g. because of wave action) was replaced.

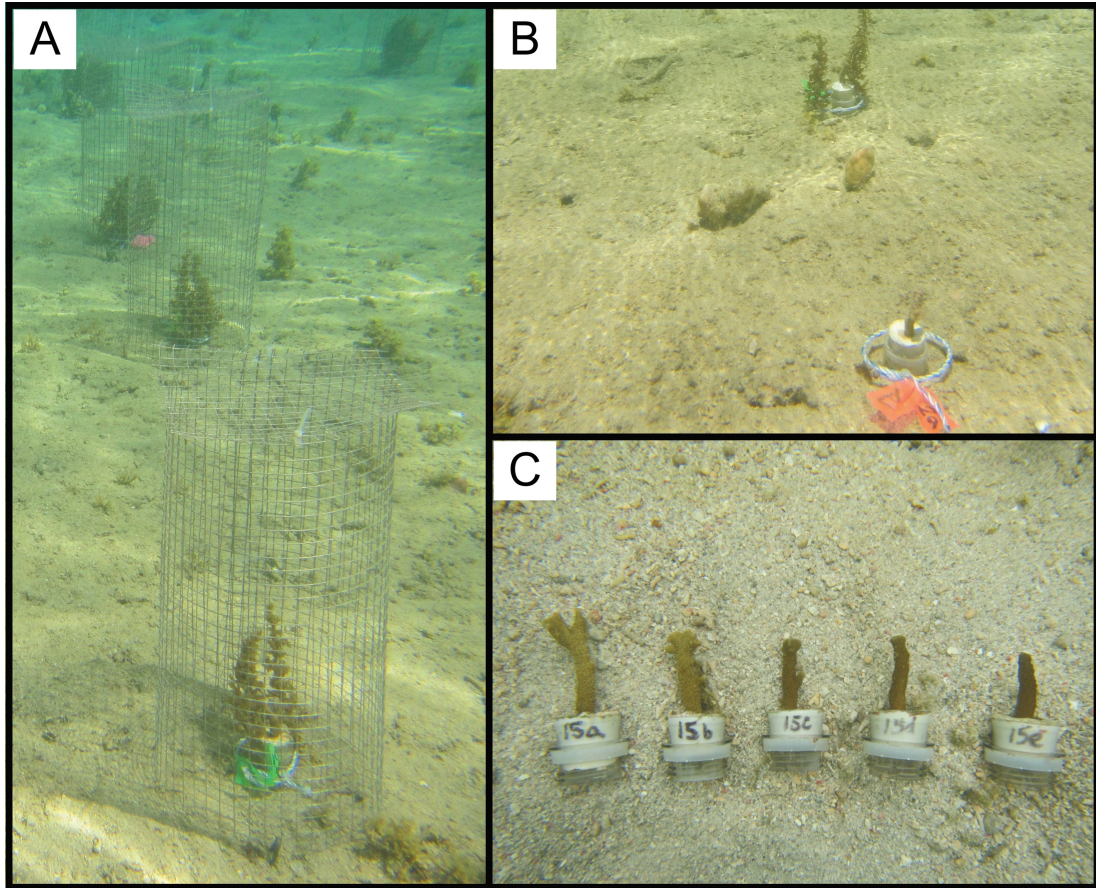


Figure 2.1: Experimental design. (A) Caged coral-algal pairs used in the coral growth experiment. (B) Coral replicates showing the bottle neck/cap and rope methods used for planting corals and applying the algal treatment. (C) Coral replicates exposed to one of five algal treatments: 0, 2, 4, 6, or 8 algal fronds (15a, 15b, 15c, 15d, and 15e respectively; ~8 weeks of exposure).



Coral growth was assessed monthly by weighing corals and their respective bottle-top/epoxy to determine the change in mass from initial measurements. Corals were weighed in the field using an electronic scale (OHAUS Scout Pro) enclosed within a plastic container mounted to a tripod holding it above the water. Bottle-tops and epoxy were brushed clean of fouling organisms within 24 h before each weighing session, and were gently shaken 30 times to remove excess water immediately prior to weighing. At the end of the experiment, each coral was separated from its bottle-top/epoxy base, and both were weighed separately to determine by subtraction the per cent change in coral mass alone. Data on percentage change in mass violated parametric assumptions, so analyses were by Kruskal–Wallis ANOVA on ranks followed by Wilcoxon pairwise comparisons corrected for multiple contrasts.

### ***Influence of seaweed on *Acanthaster* feeding preference field survey***

To assess whether the presence of *Sargassum* influenced *Acanthaster* foraging in the field, we surveyed *Acanthaster* attacks on corals with varying levels of algal contact found within Votua Reef’s fished area during July-August of 2013. We used the fished instead of the protected area because macroalgae were more common here and gave a larger range of algal-coral contacts to evaluate; in the protected area, seaweeds were too uncommon to allow this evaluation. We searched for *Acanthaster* that had recently attacked a *Montipora* colony by locating corals with characteristic *Acanthaster* feeding scars, which are white in coloration, not yet showing colonization by diatoms or filamentous algae, and thus indicative of recent predation events (Kayal et al. 2012b). Each recently attacked colony ( $n = 22$ ) was then photographed, along with the five nearest-neighbor *Montipora* colonies (all neighboring colonies were within 2 m of the

primary colony; 132 colonies in total; 15 of the nearest-neighbor colonies had also been attacked to some extent). Colony photographs were then analyzed for the percentage cover of macroalgae (with the vast majority being *Sargassum*) using Coral Point Count (Kohler and Gill 2006). The program randomly placed 40 points on each photo, and the organism beneath each point was identified.

To evaluate the relationship between the percentage of each *Montipora* colony covered by macroalgae and the percentage of each colony eaten by *Acanthaster*, we used Spearman's rank correlation because data did not meet normality assumptions. Logistic regression analysis was used to determine whether macroalgal cover (primarily *Sargassum*) influenced the probability of a colony being either attacked or not attacked. We also pooled all surveyed corals that had been either attacked or not attacked by *Acanthaster* and compared the average percentage cover of macroalgae (mostly *Sargassum*) on attacked versus non-attacked colonies. We evaluated these data using a Wilcoxon rank sum test because the data violated parametric assumptions.

### ***Feeding experiments***

To experimentally evaluate the impact of seaweed presence on *Acanthaster* feeding, we conducted a series of feeding choice experiments during July-August 2012 and June 2013 on the reef flat of Votua Village's no-take marine reserve.

Feeding trials conducted during July-August 2012 entailed placing individual sea stars within 1.5 x 1.5 m field enclosures (n = 10) and offering them a choice of either *Montipora* surrounded by fronds of *Sargassum* (length = 15-20 cm) or *Montipora* that lacked surrounding *Sargassum*. For each series of feeding trials, sea stars were collected from Votua Reef and held within separate enclosures for at least 5 days before the

experiment. We also collected paired branches (6-8 cm each) of *Montipora* from colonies on Votua Reef within 24 h of each respective trial. Pairs of corals, each cable tied to a small piece of PVC pipe (3 cm) embedded in the substrate, were transplanted 0.5 m from each other in each enclosure. *Sargassum* contact with one coral in each cage was manipulated by placing *Sargassum* in three-stranded rope and securing the ends of this rope to small nails driven into the substrate near the treatment coral. This allowed us to manipulate seaweed density in a manner mimicking natural contacts seen in the fished area of the reef. Sea star predation on corals was monitored over the following 24-36 h, noting the first colony to be attacked and consumed. Four feeding choice experiments were conducted with *Sargassum* at densities of 2, 4, 6 or 8 fronds near the treatment coral and compared with a coral lacking adjacent *Sargassum*. To test whether physical structure alone could alter *Acanthaster* feeding preference, four parallel experiments were simultaneously conducted using biologically inert *Sargassum* mimics (plastic aquarium plants) in place of live *Sargassum*.

Following the above trials, additional choice experiments were conducted using fronds of reduced length (approx. 5 cm) to determine whether adjacent *Sargassum* suppressed *Acanthaster* feeding despite a substantial reduction in algal canopy height. Sea stars were offered a choice between *Montipora* surrounded by 6 fronds of shorter *Sargassum* (5 cm height) and *Montipora* without surrounding *Sargassum* (n = 10 pairs). A parallel experiment was simultaneously conducted using plastic *Sargassum* mimics (length = 5 cm) in the place of live seaweed (n = 10 pairs). For each feeding experiment, we used a Fisher's exact test to assess the number of replicates in which the control (no nearby *Sargassum*) versus the treatment (*Sargassum* adjacent) was attacked first. At the

end of each feeding trial, uneaten corals were returned to the reef and sea stars were sacrificed (at the request of the village environmental committee).

We conducted an additional feeding experiment in June 2013 that followed the same procedures. In this experiment, individual sea stars were offered a choice between *M. hispida* and *P. cylindrica* that both lacked surrounding *Sargassum* ( $n = 10$ ), or a choice between *Montipora* surrounded by 8 fronds of *Sargassum* (length = 15-20 cm) and *Porites* that lacked surrounding *Sargassum* ( $n = 10$  pairs). *P. cylindrica* is a common coral on both healthy and degraded reefs in Fiji (Bonaldo and Hay 2014), and is typically avoided by *Acanthaster* (De'ath and Moran 1998, Pratchett 2007). Sea star predation on corals was monitored over the following 1-10 days, noting the first colony to be attacked and consumed. For each feeding trial, differences in the instances of *Montipora* versus *Porites* being attacked first were tested using a Fisher's exact test.

## Results

*Montipora* growth decreased linearly with increasing *Sargassum* density (Kruskal-Wallis ANOVA on ranks:  $H = 53.4$ ,  $df = 4$ ,  $p < 0.001$ ; Figure 2.2); control corals without *Sargassum* grew ~2.7 times more than corals surrounded by 8 *Sargassum* fronds. Although *Sargassum* suppressed *Montipora* growth (Figure 2.2), it also provided protection from *Acanthaster* predation (Figure 2.3). In field surveys, extent of *Acanthaster* predation on *Montipora* was negatively correlated with macroalgal cover (Spearman's rank correlation:  $r_s = -0.655$ ,  $p < 0.001$ ; Figure 2.3). Of the 132 colonies of *Montipora* we surveyed, 35 had been attacked and 97 had not. Attacked colonies had an average macroalgal cover of 8%, while the unattacked colonies had an average cover of 55% macroalgae (Wilcoxon rank sum test:  $z = -7.235$ ,  $p < 0.001$ ; Figure 2.3, inset). The

logistic regression model corroborated these findings by showing that the probability of *Acanthaster* predation on *Montipora* decreased with increasing cover of macroalgae (Likelihood Ratio Test:  $\chi^2 = 70.373$ ,  $df = 1$ ,  $p < 0.001$ ; Figure 2.4). Probability of being attacked dropped to approximately 0% once macroalgae covered about 40% of the coral surface.

In feeding experiments, coral colonies surrounded by 8, 6, or 4 *Sargassum* fronds were rarely, if ever, attacked, while paired corals without *Sargassum* were uniformly consumed (Figure 2.5). Attack frequency on corals with 2 adjacent *Sargassum* fronds was 50% less than corals with no adjacent *Sargassum*, but this difference was not significant ( $p = 0.174$ ). Much of the defensive value of *Sargassum* appears to derive from physical structure alone; corals surrounded by plastic *Sargassum* mimics also were significantly less susceptible to *Acanthaster* attack (Figure 2.5, right side). In 9-10 of the 10 replicates in each experiment, a coral was attacked and consumed within the initial 24-36 h.

In the feeding experiments using short (length = 5 cm) *Sargassum* fronds, coral colonies surrounded by *Sargassum* were never attacked first, while paired corals lacking *Sargassum* were uniformly attacked and consumed (Figure 2.6, left side). Similarly, corals surrounded by plastic *Sargassum* mimics of reduced height were attacked and consumed significantly less than colonies that lacked mimics (Figure 2.6, right side). In every replicate, a coral was attacked and consumed within the initial 24-48 h. When offered corals alone, *Acanthaster* always preferred *Montipora* to *Porites* ( $p < 0.001$ ; Figure 2.7, left side). If *Sargassum* was placed around *Montipora*, the preference reversed with *Acanthaster* selectively consuming *Porites* in 9 of 10 replicates ( $p < 0.001$ ; Figure 2.7, right side). Additionally, in assays where one *Montipora* colony was not

surrounded by *Sargassum*, 9 of the 10 replicates fed within 24-36 h. In contrast, when *Montipora* was surrounded by *Sargassum* and paired with *Porites*, attacks on 9 of 10 replicates did not begin until days 8-10 of the experiment, indicating the low preference of *Porites*, but the even lower preference of *Montipora* when associated with *Sargassum*.

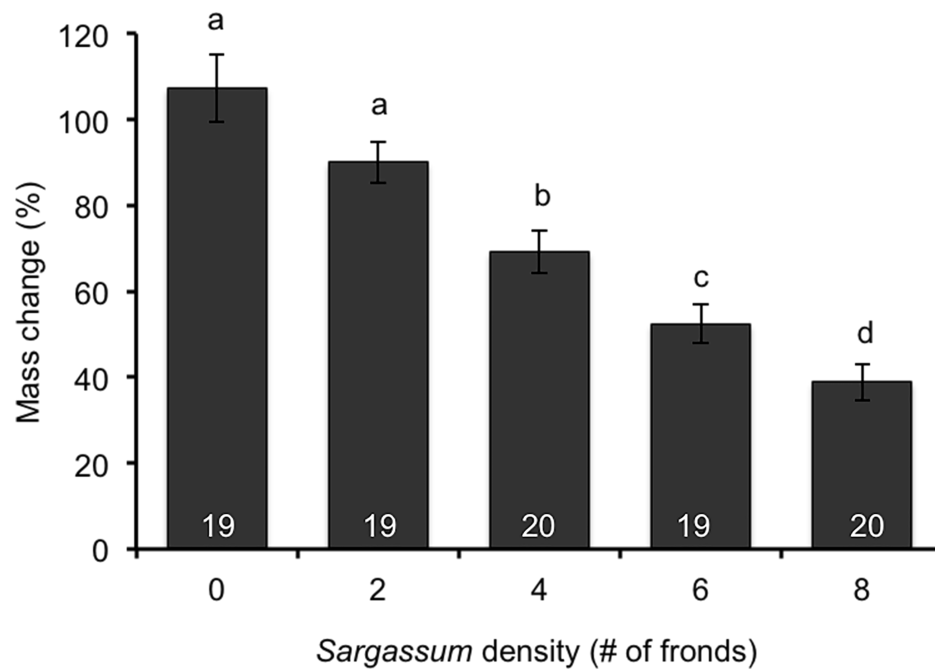


Figure 2.2: Percent change in mass during December 2013 – March 2014 for corals exposed to different densities of surrounding *Sargassum* (mean  $\pm$  SE). Analyzed by nonparametric multiple comparisons via Wilcoxon signed-rank test. Letters above bars indicate significant groupings. Numbers within bars indicate sample sizes.

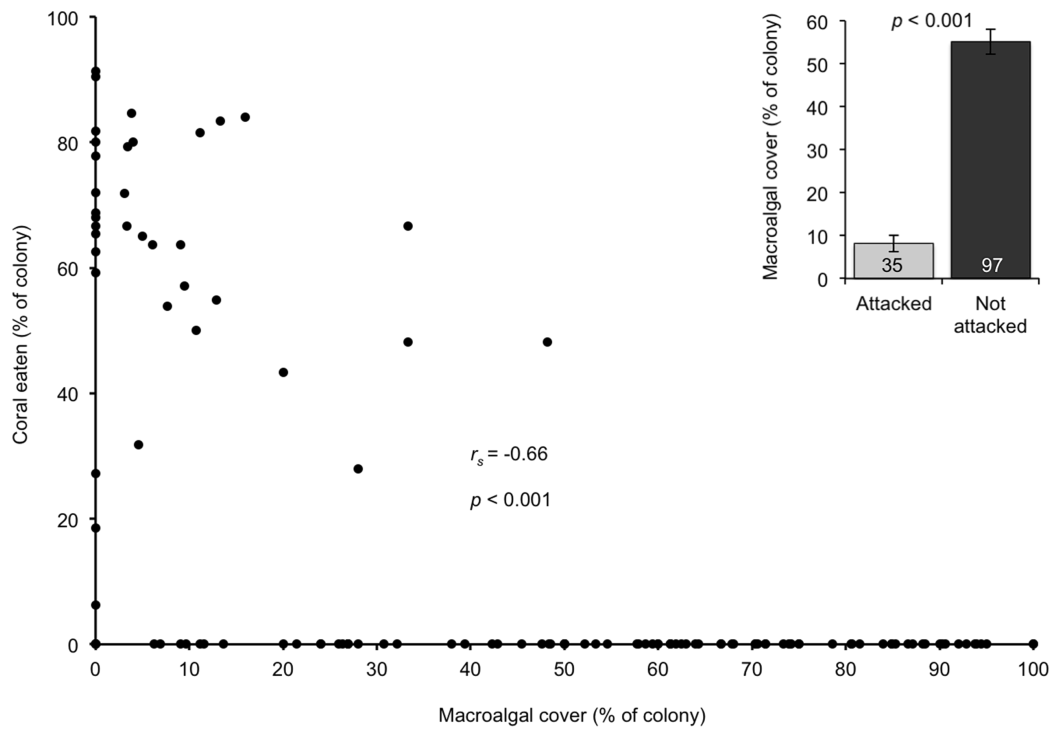


Figure 2.3: Relationship between the percent of each *Montipora* colony covered by macroalgae and the percent of each colony eaten by *Acanthaster*. Analyzed by Spearman's rank correlation. Inset: Comparison of macroalgal cover for *Montipora* colonies attacked or not attacked by *Acanthaster* (mean  $\pm$  SE). Analyzed by pairwise Wilcoxon rank sum test. Numbers within bars indicate sample sizes.



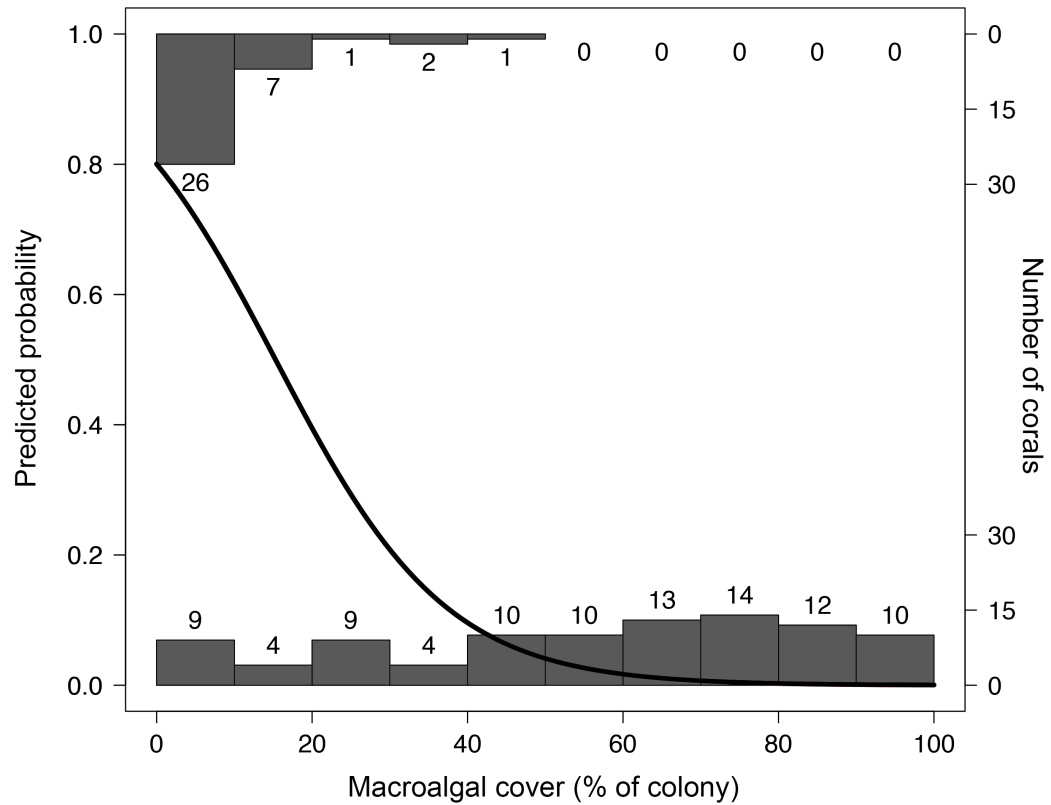


Figure 2.4: The probability of *Acanthaster* predation on *Montipora* in relation to the percent of each colony covered by macroalgae. Inland bars show histogram of the number of colonies that were either attacked (top) or not attacked (bottom) by *Acanthaster* when covered by varying amounts of macroalgae. The black line shows the fitted logistic regression curve.

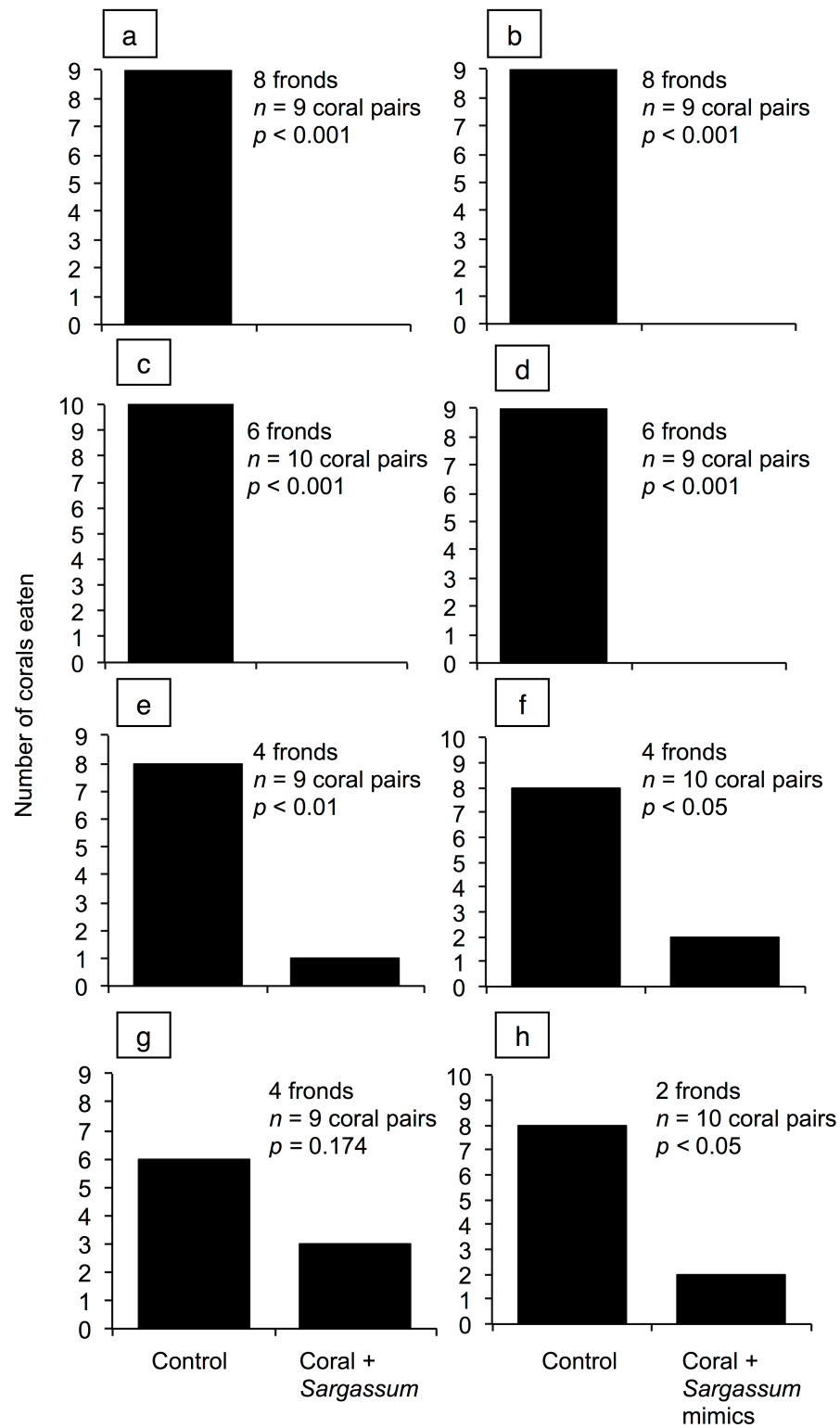


Figure 2.5: The number of *Montipora* colonies without or with *Sargassum* (left graphs) or *Sargassum* mimics (right graphs) that were attacked and consumed by *Acanthaster*, as a function of decreasing (top to bottom) *Sargassum*/*Sargassum* mimic density (a-f).

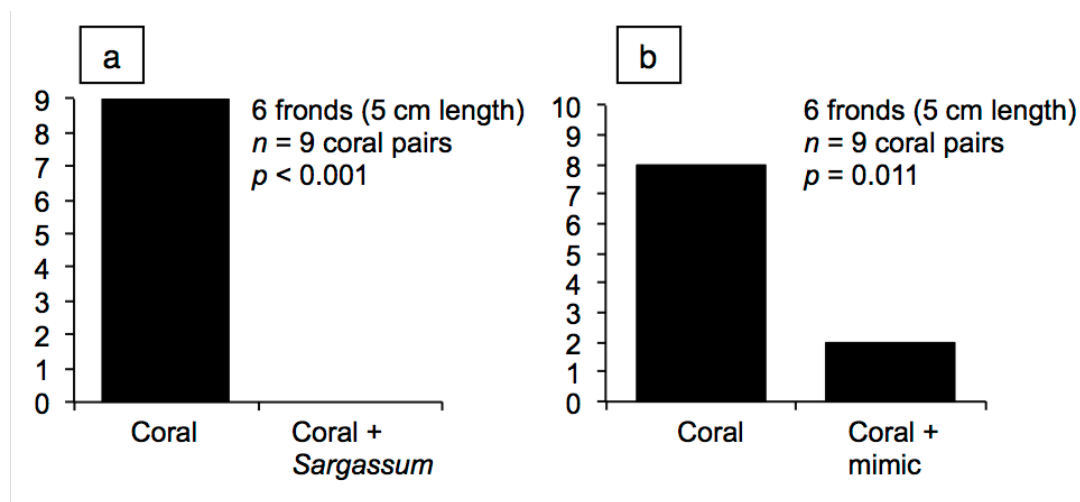


Figure 2.6: The number of *Montipora* colonies with or without shorter (5 cm) *Sargassum* (a) or *Sargassum* mimics (b) that were attacked and consumed by *Acanthaster*.

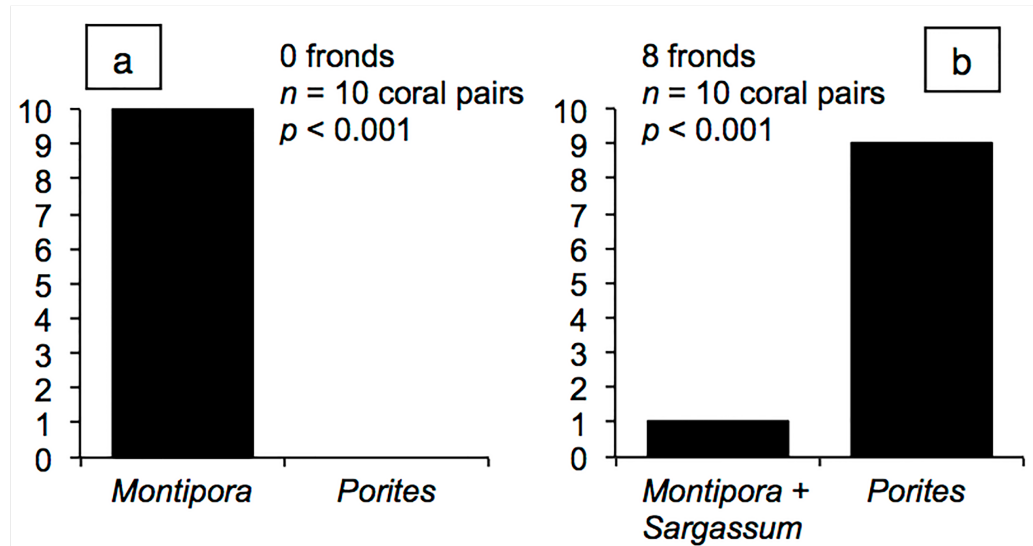


Figure 2.7: (a) The number of *Montipora* or *Porites* colonies without *Sargassum* that were attacked and consumed by *Acanthaster*. (b) The number of *Montipora* colonies with *Sargassum*, or *Porites* colonies without *Sargassum*, that were attacked and consumed by *Acanthaster*. Analyzed by Fisher's Exact Test.

## Discussion

Coral-macroalgal interactions are fundamental to coral reef community dynamics (Mumby and Steneck 2008), but research to date has mostly emphasized the many negative effects of macroalgae on corals (McCook et al. 2001, Birrell et al. 2008, Rasher and Hay 2010, Nelson et al. 2013, Wolf and Nugues 2013). In this study, we demonstrate that indirect positive effects may offset some of the direct negative effects of macroalgae on corals. Our findings underscore the need to consider the complex matrix of indirect effects that arise when species interact not as pairs but within a diverse biotic matrix involving scores of additional species. It is not uncommon for interactions that are negative in some situations to become positive in other circumstances (Bruno et al. 2003, Hay et al. 2004). Because coral-macroalgal interactions are critical in structuring modern, human-disturbed reefs (Bellwood et al. 2004, Mumby and Steneck 2008, Hughes et al. 2010), gaining a better understanding of how environmental context alters these interactions is important for both fundamental ecology and effective management.

*Sargassum* commonly blooms on reefs where herbivorous fishes have been excluded or overfished (Lewis 1986, Hughes et al. 2007, Rasher et al. 2013), and *Montipora* growth declined substantially with increasing *Sargassum* density. The mechanism(s) by which *Sargassum* reduced *Montipora* growth were not addressed, but may be physical (e.g. shading, abrasion, sediment trapping), and/or chemically- or microbially-mediated (Nugues et al. 2004, Smith et al. 2006a, Steve and Peter 2007, Birrell et al. 2008, Hauri et al. 2010, Rasher et al. 2011, Vega Thurber et al. 2012). Prior studies conducted on these same reefs detected no evidence that *Sargassum*, its lipid-soluble extracts, or inert *Sargassum* mimics caused bleaching or visible damage to

common corals (Rasher and Hay 2010, Rasher et al. 2011, Bonaldo and Hay 2014, Rasher and Hay 2014) (and we noted no bleaching effects in this assay either), but previous assays did not evaluate effects on coral growth. Our findings are consistent with earlier studies that report reductions in coral growth due to competition with *Sargassum* sp. (Edmunds and Carpenter 2001, Venera-Ponton et al. 2011) and suggest that effects of *Sargassum* on corals may be subtle, take time to manifest, and be expressed as effects on growth rather than short-term bleaching or survivorship.

Despite the adverse effects of *Sargassum* on *Montipora* growth, *Sargassum* can provide an unappreciated benefit to corals by producing an associational refuge from *Acanthaster* predation, which is a significant driver of coral decline on Pacific reefs (De'ath et al. 2012). Our field survey of *Acanthaster* feeding indicated that the frequency of sea star attacks on *Montipora* declined as association with seaweeds increased. Additionally, corals that were attacked suffered less damage as the cover of *Sargassum* increased. Thus, *Sargassum* has the potential to decrease the risk of *Acanthaster* attack, as well as the extent of colony damage to those corals that are attacked. The latter not only gives corals an opportunity to survive and recover, but may also allow for induced defenses among corals that have this ability (Gochfeld 2004).

Previous investigations on this reef flat found that about 65% of the corals in the fished area were in contact with macroalgae, that about 40% of their perimeter was in contact with macroalgae, and that corals were more frequently in contact with *Sargassum*, and the brown seaweed *Turbinaria*, than would be expected by chance (Bonaldo and Hay 2014). These patterns might be explained by our findings that contact with these non-allelopathic, but competing, macroalgae might provide a net benefit to

corals by alleviating *Acanthaster* predation, and possibly other biological or physical stressors (e.g. ultraviolet radiation or fish predators) (Jompa and McCook 1998, Bulleri et al. 2013). Given the context-dependent nature of *Montipora-Sargassum* interactions, the extent of similar benefits for other corals will likely vary as a function of coral palatability, macroalgal allelopathy, tolerance for macroalgal contact, and intensity of *Acanthaster* predation. For example, *Sargassum* contact may provide a net positive effect for corals favored by *Acanthaster* (e.g. *Acropora* or *Montipora* sp.) when sea star density is low to intermediate, while corals typically avoided by *Acanthaster* (e.g. *Porites* sp.) may benefit only when seastar density is high and preferred prey have been extirpated.

The relevance of our field survey (which assessed cover by all macroalgae) was further supported by the feeding choice experiments demonstrating that *Sargassum* by itself was capable of providing an associational refuge from *Acanthaster* predation. Interestingly, the only density of *Sargassum* (i.e. 2 fronds) that did not effectively deter *Acanthaster* was also the only density that did not significantly reduce coral growth, suggesting that the density of *Sargassum* necessary to effectively deter *Acanthaster* predation may necessarily entail coral-algal competition sufficient to reduce *Montipora* growth.

Judging by the similar effects of both *Sargassum* and plastic *Sargassum* mimics on *Acanthaster* feeding, deterrence of *Acanthaster* may be explained by the physical presence of a non-food species alone. Other researchers have documented instances where structural refuge provided by competitors (e.g. corals) or epibionts (e.g. amphipods) can reduce predation on associated corals by hindering *Acanthaster*'s ability to detect, access, and/or efficiently feed on potential prey (Glynn 1985, Devantier et al.

1986, Kayal et al. 2011, Bergsma 2012). *Sargassum* is a tough, abrasive, canopy-forming macroalga that often occurs in dense stands capable of surrounding or covering coral colonies, thus physical effects alone could be mediating coral-sea star interactions. However, our data do not preclude some aspects of chemical interference as well. *Acanthaster* feeding preferences, both within and among coral species, play an integral role in determining the effects of *Acanthaster* on coral communities (Pratchett et al. 2009, Kayal et al. 2012a). Additional choice feeding experiments revealed that the deterrent effects of *Sargassum* were not only capable of influencing *Acanthaster*'s intraspecific feeding preference for *Montipora*, but also between *Montipora* and *Porites cylindrica*. Previous studies document that *Montipora* is a preferred prey and *Porites* among the least preferred foods of *Acanthaster* (De'ath and Moran 1998, Pratchett 2007, Pratchett et al. 2009, Kayal et al. 2011, Tokeshi and Daud 2011). In our assays, sea stars overwhelmingly preferred *Montipora* when given a choice between *Montipora* and *Porites* without surrounding seaweeds, but this preference reversed when offered *Porites* alone vs *Montipora* surrounded by *Sargassum*. In this experiment, *Acanthaster* also delayed all feeding for several days before finally accepting *Porites*. These results are a striking demonstration of *Sargassum*'s ability to facilitate a trait-mediated indirect interaction by modifying *Acanthaster* feeding behaviour (i.e. TMII, *sensu* Abrams 1995).

Our results provide a novel example of how the indirect effects of coral-algal competition can potentially cascade to affect the wider coral community; however, the community-level effects of these processes are difficult to predict due to the context dependent nature of the outcomes. The associational refuge provided by *Sargassum*



appears to be predominantly physical in nature and is likely capable of providing comparable benefits to other coral species in close contact with this macroalga. There is no evidence that *Sargassum* is associated with certain coral species more than others, but recent work suggests that a broad range of coral genera show a mild positive association with *Sargassum* in the field on the reefs we studied (Bonaldo and Hay 2014).

Interspecific indirect effects such as prey switching may therefore not become prevalent until preferred coral species that lack algal contact have been depleted. *Sargassum* could then facilitate short-term apparent competition (Holt and Kotler 1987) between remaining preferred corals and less preferred species that lack macroalgae via increased *Acanthaster* predation on the latter.

Our findings complicate community-level predictions for reef systems composed of mosaics of healthy and degraded coral reef habitats, such as healthy reefs in reserves that are surrounded by fished and degraded areas along Fiji's Coral Coast. For the reefs we studied, macroalgal cover and contact with corals is higher, and coral cover lower, in fished areas that are degraded than in neighboring reserves (Rasher et al. 2013, Bonaldo and Hay 2014). Low prey availability can intensify *Acanthaster* foraging behaviour (Keesing and Lucas 1992) and is expected to result in hunger-mediated directional movement of individuals from areas of depleted coral cover to neighboring locales with higher coral cover (Ormond et al. 1973, Kayal et al. 2012a, Suzuki et al. 2012). Extensive contact between corals and fleshy macroalgae like *Sargassum* may exacerbate this behaviour by restricting access to corals that would otherwise be available, potentially leading sea stars to increase their density and predation intensity on corals in nearby MPAs if *Acanthaster* selectively migrate to, and accumulate in, habitats with more corals

and limited macroalgae. Thus, while the indirect effects of macroalgal contact may provide fitness advantages to individual colonies in degraded areas, they could also compromise adjacent coral communities composed of preferred prey species if coral predators preferentially immigrate to these areas due to the greater availability and accessibility of preferred coral prey (Kayal et al. 2012b). Our argument contrasts with previous findings documenting decreased frequency of *Acanthaster* outbreaks in no-take zones on the Great Barrier Reef (Sweatman 2008). We suspect that such patterns may vary with reserve size or the degree of degradation of surrounding reef areas.

This study highlights how interactions between corals and benthic macroalgae can be diverse and can change in direction and magnitude of effect with changing ecological context. While the negative effects of algal competition have been extensively documented (Birrell et al. 2008, Rasher et al. 2011, Barott and Rohwer 2012, Bonaldo and Hay 2014), our understanding of the dynamic and context dependent nature of these interactions when coupled with other disturbances, such as corallivory, remains limited (Mumby 2009, Venera-Ponton et al. 2011, Bulleri et al. 2013, Wolf and Nugues 2013). This is especially true for corallivorous species as influential as *Acanthaster*, which is capable of drastically reducing the functioning and productivity of reef ecosystems (Kayal et al. 2012a) and is considered to be a primary driver of long-term coral decline in locales across the Indo-Pacific (Bruno and Selig 2007, De'ath et al. 2012). The ability of macroalgae to act as an associational refuge by altering *Acanthaster* predation is an unforeseen effect that may impact reef structure, function, and resilience.

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## Chapter 3

### SIZE MATTERS: PREDATOR OUTBREAKS THREATEN FOUNDATION SPECIES IN SMALL MARINE PROTECTED AREAS

#### Abstract

The unanticipated impacts of consumers in fragmented habitats are frequently a challenge for ecosystem management. On Indo-Pacific coral reefs, crown-of-thorns sea stars (*Acanthaster* spp.) are coral predators whose outbreaks cause precipitous coral decline. Across large spatial scales, *Acanthaster* densities are lower in large no-take Marine Protected Areas (MPAs) and reefs subject to limited human exploitation. However, using a combination of observational and manipulative experiments, we found that *Acanthaster* densities within a network of small, no-take MPAs on reef flats in Fiji were ~2-3.4 times greater inside MPAs than in adjacent fished areas and ~2-2.5 times greater than the upper threshold density indicative of an outbreak. This appeared to result from selective *Acanthaster* migration to the coral-rich MPAs from fished areas that are coral-poor and dominated by macroalgae. Small MPAs can dramatically increase the cover of foundation species like corals, but may selectively attract coral predators like *Acanthaster* due to greater food densities within MPAs or because the MPAs are too small to support *Acanthaster* enemies. As coral cover increases, their chemical and visual cues may concentrate *Acanthaster* to outbreak densities that cause coral demise, compromising the value of small MPAs. An understanding of predator dynamics as a function of habitat type, size, and fragmentation needs to be incorporated into MPA design and management.

## **Introduction**

The increasing frequency and severity of anthropogenic impacts throughout the global ocean has led to habitat degradation, fragmentation, and trophic downgrading of marine ecosystems worldwide (Estes et al. 2011, McCauley et al. 2015). To counter these trends and promote ecosystem recovery and resilience, Marine Protected Areas (MPAs) are increasingly being established – often with broadly defined goals oriented towards the protection of foundation species (e.g. coral, kelp, seagrass, mangroves, etc.) upon which a broad variety of other species depend (Lubchenco et al. 2003). Efforts to establish MPAs have been particularly urgent on tropical coral reefs, which have experienced dramatic declines in coral cover and coral-associated species (Gardner et al. 2003, Bruno and Selig 2007, Carpenter et al. 2008, De'ath et al. 2012) and in numerous cases have transitioned from structurally complex systems dominated by corals to structurally simplified systems dominated by macroalgae (Mumby and Steneck 2008, Hughes et al. 2010).

While the number of MPAs worldwide has steadily increased, MPA design and management strategies are variable, with many no-take MPAs being small habitat fragments embedded within a broader background of exploited, and often degraded, habitat (Costello and Ballantine 2015). Indeed, an explicit aim of many MPAs is to aid the rehabilitation of surrounding degraded areas via spillover of adults and export of larvae (Russ and Alcala 2011). There is considerable debate over how size affects MPA performance, but much of this has focused on how size influences protection from human exploitation (e.g. incorporating species' home ranges and migration) and replenishment of focal species populations (e.g. larval export, recruitment, and spillover) (Roberts et al. 2003, Claudet et al. 2008, Gaines et al. 2010). In contrast, the effects of reserve size on

predator densities or behaviors have rarely been addressed, despite the ability of consumers to destabilize species and community-level dynamics – especially if they attack foundation species or ecosystem engineers (Estes et al. 2011, Christianen et al. 2014). Because predators have dramatic direct and indirect impact on community structure and function (Estes et al. 2011, Ohgushi et al. 2012), predicting and mitigating predator-induced disturbances are necessary to safeguard ecosystem integrity and will be increasingly important as global-scale stressors continue to challenge the effectiveness of local management efforts (Rocha et al. 2015, Scheffer et al. 2015).

A major driver of the recent 50% loss in coral cover along the Great Barrier Reef and on reefs throughout the tropical Pacific is predation by the crown-of-thorns sea star (*Acanthaster* spp.) (Bruno and Selig 2007, De'ath et al. 2012), which exhibits population outbreaks that can reduce live coral over vast areas and can lead to the ecological collapse of entire reef systems (Kayal et al. 2012). *Acanthaster* outbreaks are hypothesized to occur via several mechanisms, including (i) reduced population constraints (e.g. predation) that contribute to one or successive mass recruitment events and/or (ii) concentrated aggregations of foraging adults (for review, see (Pratchett et al. 2014)). *Acanthaster* adults use a combination of chemical and visual sensory cues to navigate toward preferred corals (Barnes et al. 1970, Ormond et al. 1973, Sigl et al. 2016), and during outbreaks, have been shown to aggregate on corals being eaten by conspecifics (Moran and Death 1992) and move en masse from areas of depleted coral to unexploited reef tracts in search of food (Moran and Death 1992, Kayal et al. 2012). There is also correlative evidence across large spatial scales that limited or restricted fishing is associated with low densities of *Acanthaster* – hypothetically due to the

maintenance of intact food webs that exert top-down control on *Acanthaster* populations (Dulvy et al. 2004, Sweatman 2008). However, despite these correlations over large areas (Dulvy et al. 2004) and long time periods (Sweatman 2008), the identity of critical predators and the life-stage of *Acanthaster* on which they feed remain unknown, and therefore speculative as a mechanism of population control.

Retention of food-web connections, along with other fisheries and conservation benefits, have been touted in the literature and used to advocate for MPAs (Lubchenco et al. 2003, Graham et al. 2011), which are now one of the most widespread management tools used by coastal communities throughout the Pacific (Jupiter et al. 2014). Despite their general success (Lester et al. 2009, Selig and Bruno 2010), some MPAs appear ineffective and can even hasten degradation of remaining critical habitat if they lead to unexpected consumer impacts on foundation species (Claudet et al. 2008). Studies from terrestrial systems emphasize that habitat fragmentation can lead to mesopredator outbreaks via reduced top-down and bottom-up population constraints (Crooks and Soule 1999, Prugh et al. 2009), but these insights have received limited attention in planning and management of MPAs, especially as a function of size and of being embedded within increasingly fragmented and degraded marine ecosystems. Most MPAs are small ( $< 1.0 \text{ km}^2$ ) (Costello and Ballantine 2015) – with management focused almost solely on various forms of fishing restrictions (e.g. permanent, partial or periodic restrictions) (Jupiter et al. 2014). Here, we provide evidence that small reserves can be at special risk for predator (*Acanthaster* spp.) outbreaks and suggest that the probability of outbreak densities may increase as conservation succeeds at increasing coral cover and thus food for, and attraction of, *Acanthaster*.

## Materials and Methods

### *Study area*

This study was conducted within paired fished and no-take MPAs on reef flats (depth of ~0-2 m at low tide and ~1-3+ m at high tide) adjacent to Namada, Vatu-o-lalai, and Votua villages along the Coral Coast of Viti Levu, Fiji (18° 13.059'S, 177° 42.979'E) (Figure 3.1). Paired areas were located within an 11 km stretch of fringing reefs that are separated by a series of deep-water channels. MPAs within this reef system are small (0.45-0.78 km<sup>2</sup>) and separated by ~2.6-10 km. MPAs exhibited high coral cover (~38-56%) and low macroalgal cover (~1-3%) on hard substrates (Rasher et al. 2013, Bonaldo and Hay 2014), as well as higher biomass and diversity of herbivorous and piscivorous fishes often targeted by artisanal fishers (Clements et al. 2012, Rasher et al. 2013). Conversely, adjacent fished areas were relatively degraded with low coral cover (4-16%), high macroalgal cover (~49-91%) (Rasher et al. 2013, Bonaldo and Hay 2014), and low biomass and diversity of herbivorous and piscivorous fishes (Clements et al. 2012, Rasher et al. 2013).

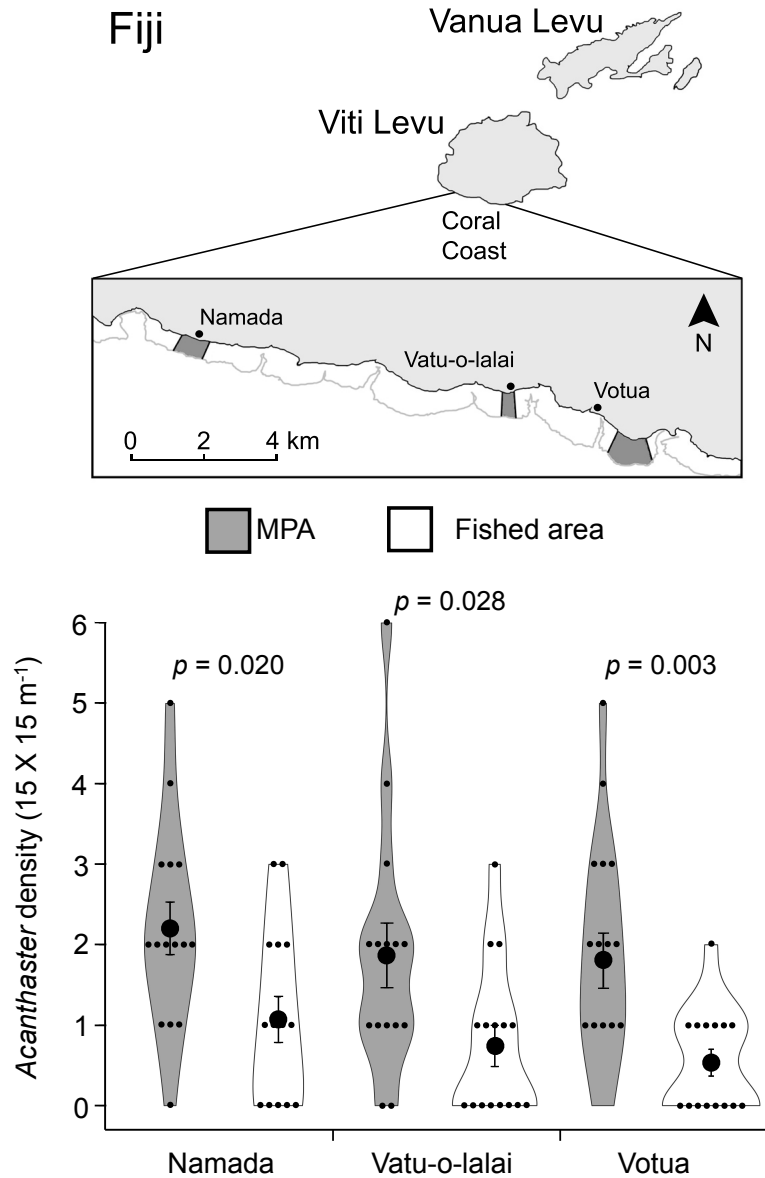


Figure 3.1: (Top panel) Village and MPA locations along the coast of Viti Levu, Fiji. Dark gray sections represent the MPAs at each site. (Bottom panel) Violin plots depicting the mean  $\pm$  SE *Acanthaster* density (large black dots and error bars), the frequency of plots with differing densities of *Acanthaster* (the enclosed areas), and each individual plot as a function of *Acanthaster* counted in that 15 x 15 m plot (small black dots) within MPAs (dark gray) and adjacent fished areas (white) at each village ( $n = 15$  quadrats reef<sup>-1</sup> location<sup>-1</sup>). Data for each pairwise comparison were analyzed using a generalized linear model (GLM) with a Poisson distribution (Votua) or quasi-GLM models (Namada and Vatu-o-lalai).

### ***Acanthaster cf. planci* density**

*Acanthaster* density was quantified in paired MPAs and fished areas using 15 x 15 m quadrats ( $n = 15 \text{ reef}^{-1} \text{ location}^{-1}$ ) that were non-overlapping and distributed haphazardly within the reef flat of each area. Surveys entailed a single snorkeler carefully searching for *Acanthaster* within and under rock ledges and coral colonies within each quadrat for five minutes, especially near areas with obvious signs of *Acanthaster* feeding. *Acanthaster* abundance data violated parametric assumptions, so differences between paired MPAs and fished areas were evaluated using generalized linear models (GLM) with either a Poisson distribution (Votua) or quasi-GLM models (Namada and Vatu-o-lalai).

### ***Experimental tagging study***

To evaluate how tagging might affect *Acanthaster* behavior, we conducted preliminary experiments comparing righting ability and feeding behavior of tagged and untagged *Acanthaster* ( $n = 10 \text{ individuals treatment}^{-1}$ ) that were caged on the reef flat of Votua's MPA. Ten individuals were each tagged by inserting five plastic tag fasteners at the base of individual arms near the oral disk (Figure 3.2), and all individuals were held in individual cages on the reef flat for the 7-day duration of this experiment. Two days were allowed for tag acclimation among the treatment group before experiments were conducted. Righting ability was assessed on days 3 and 7 post-tagging by flipping individuals onto their aboral surface and measuring the time required to right themselves onto their oral surface. This was repeated three times for each individual with a 1-minute rest interval between trials. Prior to analysis, data were log transformed and tested for homogeneity of variance using Bartlett's test. Mean righting times within and between



days were compared using a two-way ANOVA. Individuals were also offered two small fragments of the coral *Montipora hispida* (~8-10 cm length) on days three and five post-tagging to assess the effects of tagging on feeding behavior. Comparisons of whether the corals offered were either both eaten or both not eaten within 24 h were conducted using a Fisher's exact test (there were no cases of only one coral being eaten).

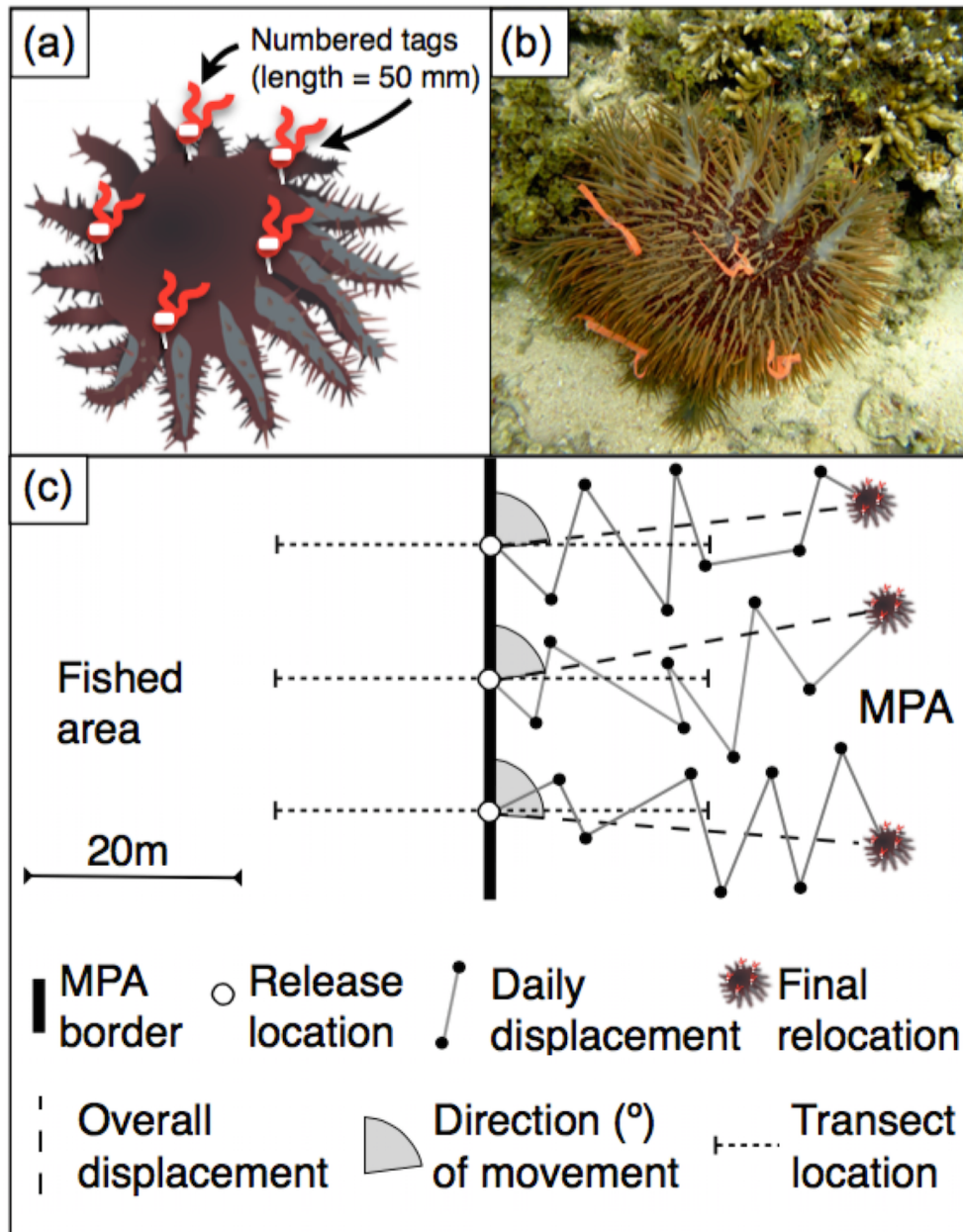


Figure 3.2: (a) Diagram of *Acanthaster* tagging and (b) photograph of a tagged *Acanthaster*. (c) Diagram of experimental design for tagged *Acanthaster* released along each MPA border and benthic surveys conducted along each MPA border. See key below diagram for symbol identification.

To test whether *Acanthaster* selectively migrated into the MPAs versus the fished areas, 120 adults of  $36 \pm 2$  cm diameter (from the tips of opposite arms) were collected from the MPAs and adjacent fished areas of reefs flats near Votua, Vatu-o-lalai, and Namada villages, with 20 individuals collected from within and 20 from outside the MPAs at each village site (40 individuals village<sup>-1</sup> site<sup>-1</sup>). Each individual was tagged with five plastic tag fasteners between the base of individual arms, and labeled flagging tape was attached to the end of each tag fastener to aid in location and identification (Figure 3.2). Individuals were then enclosed within cages located along the MPA border perpendicular to the coastline at each site (20 individuals border<sup>-1</sup> location<sup>-1</sup>) for 48 h to allow for tag acclimation. Upon release, individuals' movements were monitored at 24 h intervals for four to eight days by physically locating each individual and recording its location via GPS (Garmin GPS 76CSX). GPS coordinates of individual *Acanthaster* positions were imported into ArcMAP (Version 10.3.1), and the Geospatial Modeling Environment extension (Version 0.7.4.0) was used to calculate individuals' initial and final directions of movement relative to their release point along their respective MPA border, as well as each individual's net displacement between consecutive days (Figure 3.2). The angular directions of individuals' positions relative to the MPA border were plotted as circular data and together tested for circular uniformity against an alternative that presumes a specified angle (e.g. 90°) using Batschelet's modified Hodges-Ajne test. This analysis was conducted for both the first and final relocation of each individual because initial orientations are more suitable for evaluating patch detection capabilities (Goodwin et al. 1999, Zollner and Lima 1999).

To determine whether an individual's origin influenced their movement direction, we compared relocations, both pooled across all villages and individually for each MPA border, of *Acanthaster* collected from the MPAs and fished areas. We also characterized the path directionality of individual sea star movements at each border where data from two or more consecutive movements (relocations on  $\geq 2$  days in a row) were available using the ratio of  $D$  (the net displacement from initial to final position in the path) to  $W$  (total distance traveled between days) (Ferlin 1973, Scheibling 1981). A  $D:W$  ratio of 1 represents an individual exhibiting uniformly directional movement (i.e. straight-line path). Values  $> 0.7$  are considered highly directional,  $> 0.5$  partially directional, and  $< 0.5$  undirected (Ferlin 1973, Scheibling 1981).

#### ***MPA border benthic surveys***

Surveys of benthic community composition were conducted to assess habitat differences inside and outside of each MPA border and the relationship between coral cover and *Acanthaster* displacement at each border. Surveys used 40 m point intercept transects ( $n = 20$  transects border<sup>-1</sup> MPA<sup>-1</sup>, points at 0.5 m intervals, 1,600 points border<sup>-1</sup>) that were non-overlapping (mean distance between transects =  $\sim 12$  m) and oriented parallel to the coastline, with the midpoint (20 m) of each transect positioned on the MPA border (20 m within the MPA and 20 m within the fished area) (Figure 3.2). Benthic data from within and outside each MPA border were square root transformed if needed, and analyzed using t-tests. When benthic data could not be transformed to meet parametric assumptions, the original count data were used and analyzed with quasi-GLM models. To test for correlations between coral cover and *Acanthaster* movement among sites, coral cover along the transect at the site of each individual's release as well as pooled coral

cover by MPA border were each, separately, linearly regressed against the displacement between consecutive days exhibited by the individual sea star at that location and the mean displacement along each individual MPA border, respectively.

## Results

We found that *Acanthaster* densities within MPAs ( $\sim 80\text{-}98 \text{ ha}^{-1}$ ) were  $\sim 2\text{-}3.4$  times greater than within fished areas ( $\sim 23\text{-}47 \text{ ha}^{-1}$ ;  $p \leq 0.030$ , Figure 3.1), as well as  $\sim 2\text{-}2.5$  times greater than the upper threshold density indicative of an outbreak (40 individuals per hectare (Moran and Death 1992)). Our tagging methods affected neither righting times ( $p = 0.190$ ) nor frequencies of feeding ( $p = 1.000$ ) for *Acanthaster*; there also was no effect of assessing these behaviors on days three or seven post tagging ( $p \geq 0.719$ , Table 3.1).

Table 3.1: Two-way ANOVA on the effect of tagging on righting time of *Acanthaster* after 2 and 7 days. All data were log transformed. Bartlett test for homogeneity of variances ( $F = 0.883$ ,  $p = 0.347$ ).

Analysis of Variance					
Source	s.s.	d.f.	MS	F-ratio	p
Model	0.050	3	0.016	0.647	0.590
Error	0.934	36	0.025		
Total	0.984	39			

Effect of test					
Source	s.s.	d.f.	F-ratio	p	
Tag	0.046	1	1.786	0.190	
Day	0.003	1	0.132	0.719	
Tag $\times$ day	0.001	1	0.022	0.882	

When *Acanthaster* were released along MPA borders, their directions of initial movement were significantly biased toward the MPA for five of the six borders ( $p < 0.050$ , Figure 3.3), and suggestive of an MPA preference in the remaining contrast. Approximately 73% of all individuals released and relocated (85 of 116) moved to the MPA, a pattern that was consistent regardless of whether *Acanthaster* were originally collected from the MPAs or fished areas ( $p > 0.656$ , Table 3.2). Similarly, final movement positions were significantly biased toward MPAs for all six contrasts ( $p < 0.050$ , Figure 3.3). The ratio of net displacement ( $D$ ) to total displacement between consecutive days ( $W$ ) indicated that *Acanthaster* movement paths exhibited considerable directionality at five of the six MPA borders ( $D:W = 0.453\text{-}0.717$ , Table 3.3).

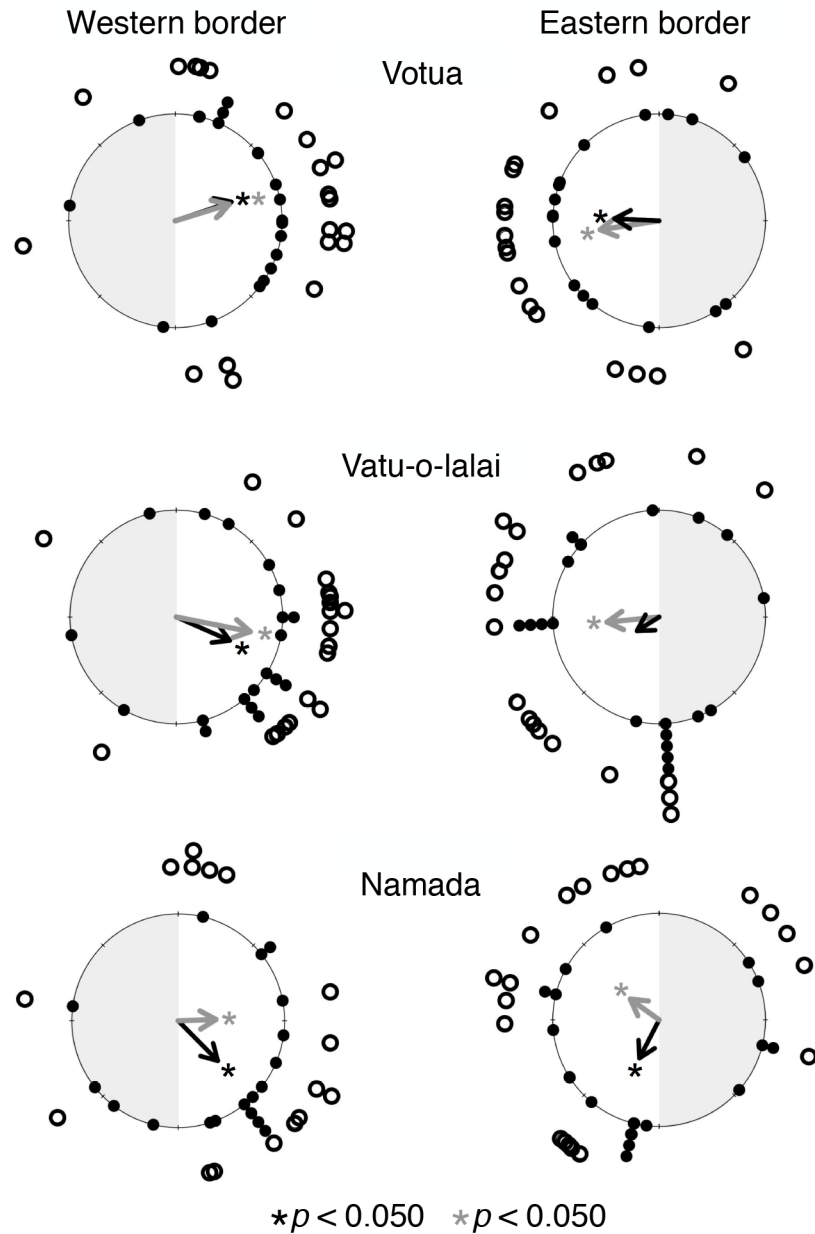


Figure 3.3: Movement directions of initial (solid dots) and final (open dots) *Acanthaster* relocations from release points at MPA/non-MPA borders on each side of the MPA at each of the three villages. Arrows represent the resultant vector (R) for initial (black) and final (gray) relocations. Black and gray asterisks indicate significant differences between *Acanthaster* movement towards MPAs (white region) rather than fished areas (shaded region) for initial and final relocations, respectively (Modified Hodges-Ajne test,  $p < 0.050$ ).

Table 3.2: Comparisons of movements of *Acanthaster* originating from the MPAs or fished areas into the MPA or fished areas at each MPA border. Comparisons between *Acanthaster* of different origins tested with Fisher's exact test.

Village	MPA boundary	COTS Origin	Into MPA (n)	Into fished area (n)	Fisher exact test
Namada	West	MPA	9	1	$p = 1.000$
Namada	West	Fished area	8	2	
Namada	East	MPA	6	2	$p = 1.000$
Namada	East	Fished area	7	3	
Vatu-o-lalai	West	MPA	8	2	$p = 1.000$
Vatu-o-lalai	West	Fished area	8	1	
Vatu-o-lalai	East	MPA	4	6	$p = 0.656$
Vatu-o-lalai	East	Fished area	6	4	
Votua	West	MPA	7	2	$p = 1.000$
Votua	West	Fished area	7	3	
Votua	East	MPA	7	3	$p = 1.000$
Votua	East	Fished area	8	2	

Table 3.3: *Acanthaster* net displacement ( $\text{m day}^{-1}$ ; mean  $\pm$  SE), displacement between consecutive days ( $\text{m day}^{-1}$ ; mean  $\pm$  SE), and  $D:W$  ratio (mean  $\pm$  SD) at MPA border locations.

Village	MPA border	Mean net displacement	S.E.	Mean consecutive day displacement	S.E.	Mean $D:W$	S.D.
Namada	West	4.128	0.466	3.905	0.749	0.717	0.303
Namada	East	9.630	1.509	5.762	0.847	0.602	0.268
Vatu-o-lalai	West	7.662	2.219	2.789	0.539	0.592	0.240
Vatu-o-lalai	East	3.893	0.493	1.187	0.201	0.453	0.248
Votua	West	5.934	0.926	1.902	0.507	0.677	0.311
Votua	East	5.052	1.726	1.436	0.293	0.651	0.355



Benthic community composition commonly differed immediately within versus outside MPAs, with coral and macroalgal cover exhibiting the most frequent significant differences across MPA borders (Figure 3.4). Coral cover 20 m within MPA borders was 80-440% greater than in the 20 m outside MPA borders, while macroalgal cover was 20-610% greater immediately outside versus inside the MPAs; differences were even more pronounced toward the centers of each area (Rasher et al. 2013). *Acanthaster* rates of displacement were negatively correlated with mean coral cover along each border, both when plotted by individual *Acanthaster* ( $R^2 = 0.209, p < 0.001$ ) and when pooled by MPA border ( $R^2 = 0.756, p = 0.030$ ; Figure 3.5).

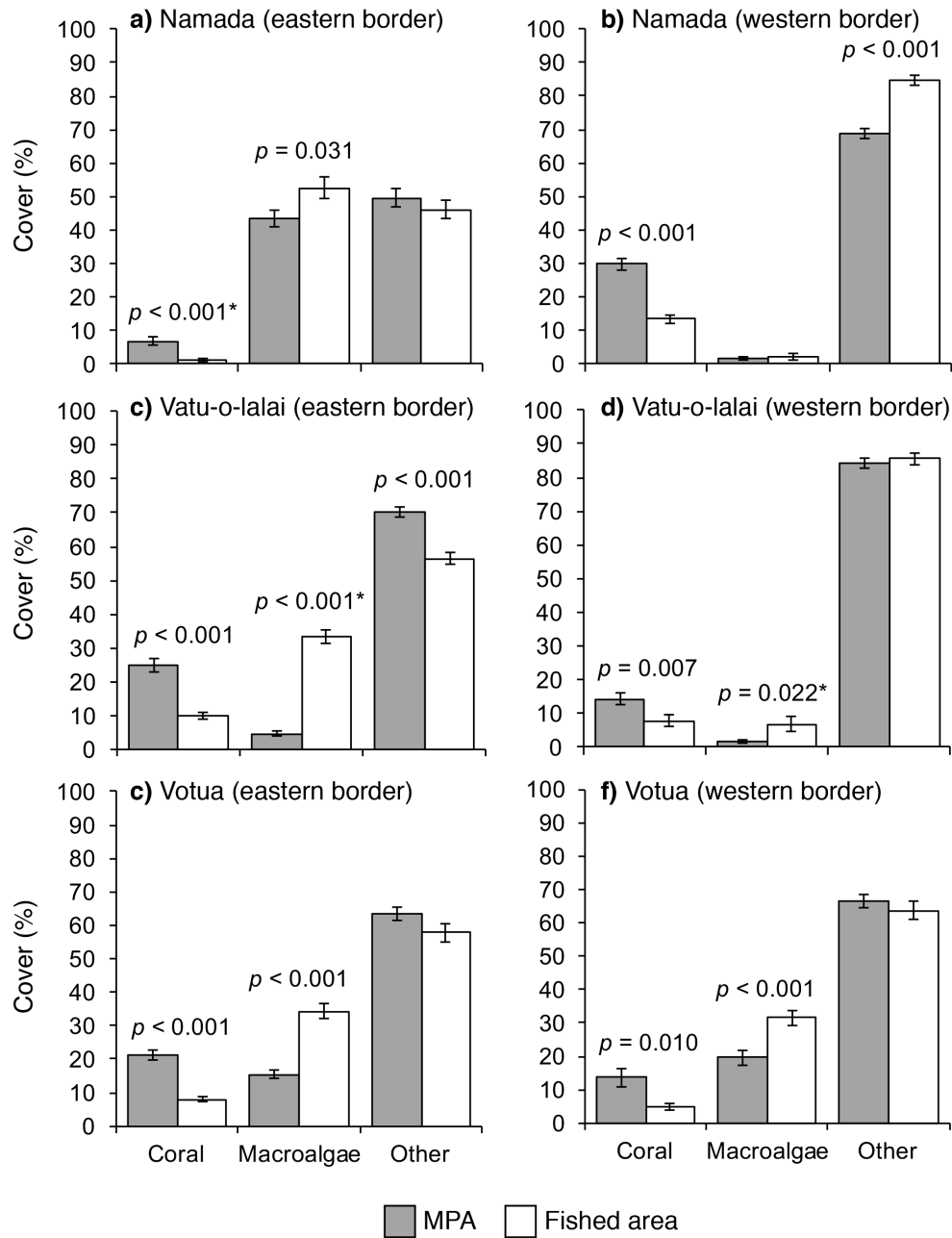


Figure 3.4: Comparisons of benthic cover (mean %  $\pm$  SE) 20 m inside (black) and 20 m outside (gray) of MPA borders perpendicular to the coastline at Namada, Vatu-o-lalai, and Votua villages ( $n = 20$  transects border<sup>-1</sup> location<sup>-1</sup>). The category “Other” includes dead coral, rock, rubble/sand, and uncommon benthic organisms (e.g. zooanthids, soft coral). Asterisks after  $p$ -values indicate comparisons analyzed with quasi-GLM models.

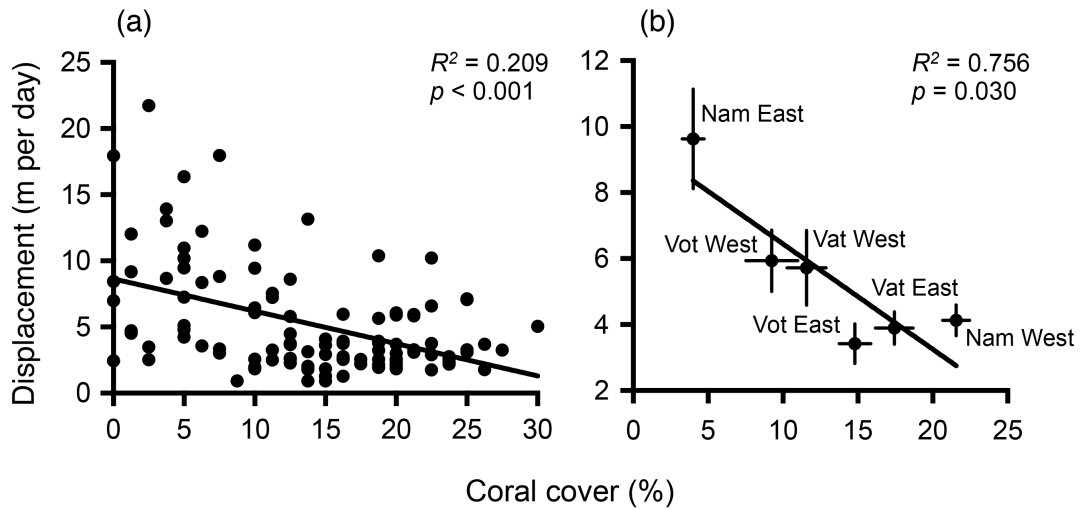


Figure 3.5: (a) Relationship between individual *Acanthaster* displacement between consecutive days ( $\text{m day}^{-1}$ ) and coral cover (%) at each individual's release location along MPA borders. (b) Relationship between coral cover (mean %  $\pm$  SE) and *Acanthaster* displacement between consecutive days ( $\text{m day}^{-1}$ ; mean  $\pm$  SE) when pooled by MPA border. See Fig 1 for village site names. Coefficients of regression ( $R^2$ ) and  $p$ -values are indicated in the graph. Two data points with extreme *Acanthaster* displacement values ( $y_1 = 42.65 \text{ m}$ ,  $y_2 = 34.39 \text{ m}$ ) at low coral cover ( $x_1 = 0\%$ ,  $x_2 = 11.25\%$ ) were excluded from analyses after performing an outlier analysis (Jackknife distances) using JMP (Version 11.0.0).

## Discussion

Our findings suggest that at small scales, common MPA benefits (e.g. increased coral cover) may attract predators such as *Acanthaster*. *Acanthaster* were 2-3.4 times as abundant within the coral-rich MPAs, exhibiting densities similar to those that have caused extensive coral decline (e.g. >50%; Pratchett et al. 2009), and lead to cascading effects on reef structure and associated species (Kayal et al. 2012). This unanticipated pattern may provide an important lesson for the management of MPAs across the Pacific, as the overwhelming majority of tropical Pacific MPAs are small (<0.5 km<sup>2</sup>; Jupiter et al. 2014) and like those in this study, are situated within a background of increasingly degraded reef habitat (Bruno and Selig 2007). Given the widespread use of small MPAs as management tools (Russ and Alcala 2011, Costello and Ballantine 2015) and the destructive impacts that *Acanthaster* feeding can have on coral reefs at the densities documented here (Pratchett et al. 2009, Kayal et al. 2012), our study highlights the need to consider how the size and placement of MPAs influence their susceptibility to *Acanthaster* outbreaks, and whether the probability of outbreaks increases with MPA success (enhanced coral cover, the foundation species for this system). Despite these high densities of *Acanthaster*, corals are still abundant in the MPAs we investigated (Rasher et al. 2013, Bonaldo and Hay 2014). This may be due to *Acanthaster* densities increasing recently and not yet strongly suppressing coral cover or due to coral growth rates on these shallow, turbulent, and well-lit platforms being high enough to generate positive net growth despite high rates of consumption.

Our findings contrast with previous studies where *Acanthaster* densities were reduced in large MPAs or areas subject to limited fishing pressure (Dulvy et al. 2004,

Sweatman 2008). Our patterns may differ from these earlier studies due to (i) small MPAs having greater perimeter to area ratios that facilitate increased movement of *Acanthaster* into coral-rich MPAs, (ii) habitat disparities between coral-rich MPAs and surrounding degraded reefs that enhance *Acanthaster* recruitment and immigration to coral-rich MPAs, (iii) differences in critical consumers or processes between MPAs located on shallow (~1-3+ m) reef flats like those we studied vs. reefs from previous studies (~7m in depth or greater), or (iv) large MPAs supporting critical consumers or processes that are not sustainable in the small MPAs we studied. That said, it is critical to note that previous studies assumed that predation suppressed *Acanthaster* densities in large MPAs or areas with reduced fishing pressure (Dulvy et al. 2004, Sweatman 2008), but this assumption was not directly tested. Neither the identities of the critical predators of *Acanthaster* nor the life stage at which predation could control *Acanthaster* have been determined. Regardless, it is evident from our tagging and density data that *Acanthaster* can selectively migrate into the coral-rich MPAs vs. the coral-poor fished areas and that predation within these reef systems is insufficient to reduce *Acanthaster* numbers to densities below those capable of causing considerable damage to coral communities. These findings highlight an important risk for the many small MPAs embedded within increasingly fragmented and degraded reef ecosystems.

Predator outbreaks may occur in small MPAs due to increased resource availability as the MPAs become effective and enhance the abundance of foundation species that serve as attractive foods for consumers (Christianen et al. 2014). Our findings build on a small, but growing, body of evidence that consumer attraction may be a critical vulnerability for effective management, as similar scenarios have been

documented in other systems, including attraction and overgrazing of seagrass MPAs by sea turtles (Christianen et al. 2014) and plant community regime shifts due to elephant aggregations in African reserves (Dublin et al. 1990, Landman et al. 2014). On coral reefs, this phenomenon may be especially problematic if degraded areas near MPAs serve as nurseries for predators such as *Acanthaster*. For *Acanthaster*, degraded areas surrounding reserves have abundant coral rubble (into which juvenile *Acanthaster* selectively recruit (Zann et al. 1987) and considerable abundance of crustose coralline algae, a favored food of juvenile *Acanthaster* (for review, see Pratchett et al. 2014). Increased juvenile survival in these degraded reef areas followed by selective migration to coral-rich MPAs could contribute to the high *Acanthaster* densities we documented within MPAs.

A second possibility, or additional contributor, to the density difference we noted is that small, fragmented systems may lack top predators, sometimes allowing mesopredators like *Acanthaster* to escape consumer control (Crooks and Soule 1999, Prugh et al. 2009, Brashares et al. 2010). Predatory fish biomass was low in both the small MPAs and the fished areas we investigated (Clements et al. 2012, Bonaldo et al. 2017) and is comparable to, or lower than, the biomass of predatory fishes on reefs previously associated with high *Acanthaster* population densities (Dulvy et al. 2004). Lower coral abundance in fished areas may also reduce predation on larval and juvenile *Acanthaster* by coral-associated planktivorous fishes, which have been shown in laboratory trials to prey upon *Acanthaster* larvae (Cowan et al. 2016). While the identity and roles of predatory fishes controlling *Acanthaster* densities in the wild are largely unknown (Dulvy et al. 2004, Sweatman 2008, Pratchett et al. 2014), it is plausible that

our predator-depauperate reefs are incapable of exerting top-down control on *Acanthaster* (e.g. predation during vulnerable pre-reproductive stages (Sweatman 2008).

Regardless of what processes normally control *Acanthaster* densities, our tagging data show that migration of adult sea stars from degraded areas could lead to outbreak densities within the coral-rich MPAs. *Acanthaster* consistently moved towards the MPAs at rates proportional to local coral density; a behavior consistent with outbreak scenarios where sea stars migrate from areas of low coral abundance and aggregate on remaining coral patches (Dana et al. 1972, Kenyon and Aeby 2009, Kayal et al. 2012). However, rather than aggregative behavior induced by recent coral decline, data from the MPAs we studied suggest that increases in live coral following MPA establishment (Rasher et al. 2013, Bonaldo and Hay 2014) are producing “food hotspots” that attract sea stars from surrounding overfished areas to form ‘spot’ outbreaks [50]. Greater herbivore control of macroalgae within MPAs (Rasher et al. 2013) may further exacerbate this hotspot effect because macroalgae suppress *Acanthaster* feeding on adjacent corals (Clements and Hay 2015), resulting in corals within the MPAs being not only more abundant and more attractive, but also more accessible to *Acanthaster* than corals in the degraded, seaweed-dominated areas surrounding the MPAs. Thus, common benefits of MPAs may become liabilities if reef spatial dynamics, consumer movements, and species interaction networks are not considered in a community context that extends beyond reserve borders.

While many outbreak densities of *Acanthaster* appear to occur following massive recruitment events (Pratchett et al. 2014), this did not appear to be the process generating outbreak densities in our sites. We did not note high densities of *Acanthaster* in the fished areas or on deeper portions of adjacent reefs. Rather than resulting from boom and bust

cycles, the high densities noted in the MPAs we studied appeared to result from lower chronic densities of *Acanthaster* aggregating in the food hot-spots generated within MPAs. Thus, these localized outbreak densities seem to be generated by different processes (Dana et al. 1972, Pratchett 2005) and to occur on different temporal and spatial scales than outbreaks noted in many previous investigations (for review, see Pratchett et al. 2014).

Optimizing local-scale management can provide a critical buffer for ecosystems subject to an increasing array of local and global disturbances (Anthony et al. 2015). Our study highlights a shortcoming of basic extraction restrictions if these are not integrated with issues of scale, migration, and food web dynamics. Across the Pacific where customary ownership and governance of marine resources occurs at a local scale, small MPAs are among the most common strategies used to manage coral reef ecosystems (Jupiter et al. 2014). When enforced, they can produce remarkably positive effects (Lester et al. 2009, Selig and Bruno 2010, Graham et al. 2011), but as positive outcomes accumulate, this success may concentrate coral predators and endanger MPA resilience. An appreciation for mechanisms generating predator outbreaks needs to be included in the conceptual toolkit of MPA managers. This is particularly relevant to small, locally-managed MPAs where control of *Acanthaster* by physical removal, injections, or other means is likely feasible (Moutardier et al. 2015). However, most MPA management strategies are limited to fishing restrictions that vary in scope and duration (e.g. permanent, partial, or periodic restrictions) (Jupiter et al. 2014) and are likely incapable of facilitating adequate biological control of *Acanthaster*. While protection from extraction may be conferring other benefits commonly expected from MPAs, the concern



is that without active management of predators like *Acanthaster*, current schemes may promote situations where predation threatens the foundation species upon which MPA success is built. This could compromise gains that have been made since reserve establishment, as well as those expected for the future.

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## CHAPTER 4

### SMALL MARINE PROTECTED AREAS PROTECT CORALS FROM THE GASTROPOD *CORALLIOPHILA VIOLACEA*, A SIGNIFICANT CORAL PREDATOR

#### Abstract

Large coral predators like the crown-of-thorns sea star (*Acanthaster* spp.) can alter the structure, persistence, and resilience of coral reef ecosystems, but the ecological impacts, and consequences for management, of smaller, less obvious corallivores remain relatively unexplored. In this study, we investigated how feeding by the corallivorous gastropod *Coralliophila violacea*, a sessile “prudent feeder” that causes only localized visual tissue damage, impacted the growth of the common Indo-Pacific coral *Porites cylindrica*. Over a 24-day trial in the field, feeding by individual *C. violacea* reduced *P. cylindrica* growth by ~18-43%, depending on snail size. Given these strong effects, we further investigated whether reef protection status influenced *C. violacea* densities on *P. cylindrica* colonies within three pairs of small Marine Protected Areas (MPAs) and adjacent fished areas in Fiji. *C. violacea* densities were 5-35 times greater within fished areas than adjacent MPAs. Analyses of *C. violacea* size-frequency distributions within MPAs and fished areas, and subsequent tethering experiments, indicated that smaller size classes were more vulnerable to predation in MPAs than neighboring fished areas. Our findings highlight the considerable, but often underappreciated, negative impacts of this common corallivore, as well as the value of the more intact food webs in MPAs as mitigators of predator outbreaks that threaten foundation species.



## Introduction

Coral reefs worldwide face numerous natural and human stressors that lead to sustained coral loss, reef community shifts, and reduced ecosystem resilience (Bellwood et al. 2004, Hughes et al. 2010). Among these, coral predators (corallivores) are increasingly recognized for their direct (e.g. consumption, disease vectoring) and cascading effects on corals and on reef community dynamics (Rotjan and Lewis 2008, De'ath et al. 2012). When reef degradation is caused by other stressors (e.g., storms, heat stress), enhanced per capita predation on remaining corals can further decrease resilience, hastening declines, preventing recovery, and facilitating phase-shifts to algal-dominated reefs (Knowlton et al. 1990, Rotjan et al. 2006, Wolf and Nugues 2013). That said, the role and impact of many corallivores on reefs at different stages of degradation remain poorly understood and a challenge for effective coral reef management (Mumby 2009).

Negative effects of predation become obvious when corallivores are overabundant, such as during population 'outbreaks' of crown-of-thorns sea stars (*Acanthaster* spp.) (Kayal et al. 2012, Pratchett et al. 2014) and *Drupella* spp. snails (Shafir et al. 2008). Both experimental and correlative studies suggest that predation can regulate corallivore densities but that this top-down forcing may be lost or suppressed if consumers are overfished (McClanahan 1989, Dulvy et al. 2004, Burkepile and Hay 2007, Sweatman 2008). Implementing no-take Marine Protected Areas (MPAs) is one strategy expected to help lessen corallivore outbreaks (Graham et al. 2011), but most MPAs are small (Costello and Ballantine 2015) and the reserve size necessary to foster top-down control remains uncertain (Sale et al. 2005, Claudet et al. 2008, D'Agata et al. 2016, Clements and Hay 2017). Furthermore, whether similar outcomes extend to other,

less well-known corallivores deserve further investigation. This is especially true as coral densities decline due to other stressors, corallivores escape predator control due to reef degradation, and the limited number, or stressed condition, of remaining corals cause them to gain the full attention of dense, food-limited corallivores (Knowlton et al. 1990, Bright et al. 2015).

In this study, we used a combination of observational and manipulative experiments to investigate the impacts of a common coral predator, the gastropod *Coralliophila violacea*, on a coral often found on degraded reefs. We also evaluated whether reef protection status influenced *C. violacea* population densities in small MPAs and adjacent fished areas in Fiji. *C. violacea* is one of the few corallivores known to feed almost exclusively on *Porites* spp., which are among those corals that exhibit lower sensitivity to a number of stressors (e.g., climate-induced bleaching, macroalgal allelopathy, crown-of-thorns predation) commonly contributing to coral decline (Pratchett 2007, Carpenter et al. 2008, Rasher et al. 2011, Bonaldo and Hay 2014). Species of *Porites* often represent one of the few remaining corals on severely damaged reefs (McClanahan and Mutere 1994, Green et al. 2008, Adjerooud et al. 2009) and as such may be especially important to maintain if total reef loss is to be prevented.

Here, we quantified: 1) the effects of *C. violacea* feeding on growth and survivorship of *Porites cylindrica*, 2) how feeding impact varied with snail size, 3) whether *C. violacea* densities on *P. cylindrica* differed between three small MPAs versus their adjacent fished areas, and 4) whether rates of predation on *C. violacea* differed between MPAs and fished areas – potentially contributing to density differences between these areas.

## Materials and Methods

### *C. violacea* densities and size frequency distributions within paired Marine Protected Areas (MPAs) vs. fished areas

Surveys assessing *C. violacea* densities on colonies of *P. cylindrica* were conducted during June 2015 within three, small, no-take MPAs and three neighboring fished reefs near Votua, Vatu-o-lalai, and Namada villages along the Coral Coast of Viti Levu, Fiji (Figure 4.1). The MPAs are ~0.78, 0.45, and 0.48 km<sup>2</sup> in total area, respectively. Paired areas are separated by ~300 m (at Votua and Vatu-o-lalai reefs) to 1700 m (at Namada reef) and are embedded within an 11 km stretch of shallow (0-3 m deep at low tide) fringing back reef lagoon with similar physical regimes (e.g. depth, current strength). Established during 2002 (Vatu-o-lalai, Namada) to 2003 (Votua), the MPAs exhibit relatively high coral cover (~38-56%) and low macroalgal cover (~1-3%) on hard substrates compared to surrounding fished areas where coral cover is low (4-16%) and macroalgal cover is high (~49-91%) (Rasher et al. 2013). Likewise, MPAs exhibit greater biomass and diversity of fishes often targeted by artisanal fishers (Clements et al. 2012, Bonaldo et al. 2017).

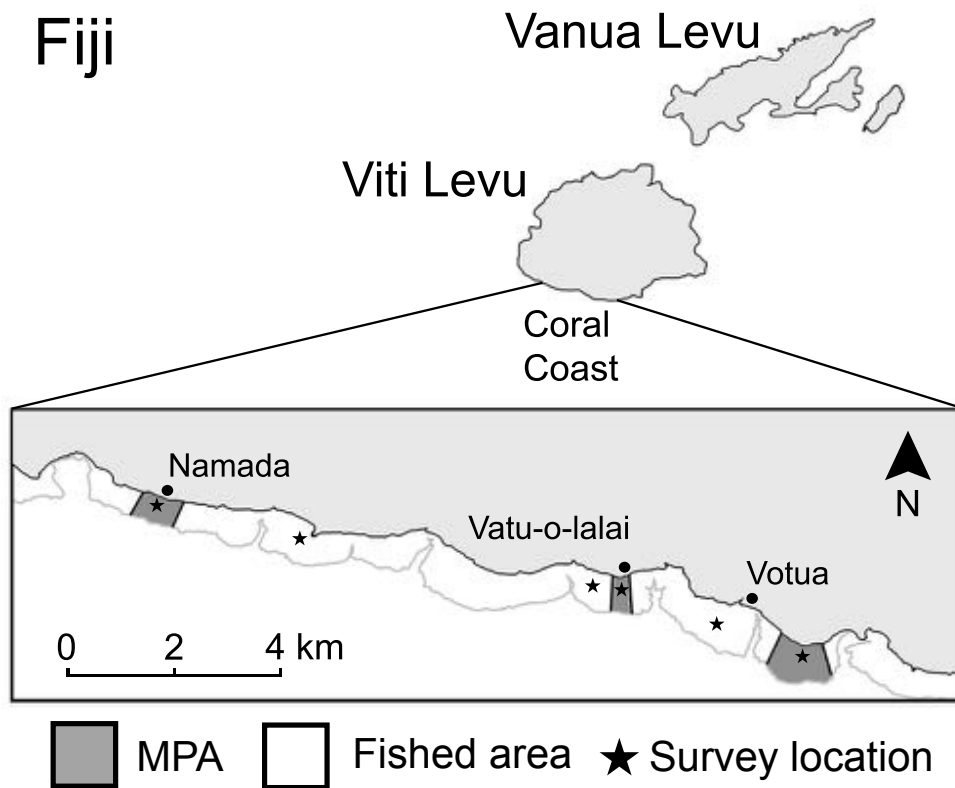


Figure 4.1: Village and MPA locations along the Coral Coast of Viti Levu, Fiji. Dark gray sections represent the MPAs at each village site; ★ indicate approximate location where fished area assays were conducted.

Differences in *C. violacea* density between the MPA and fished area at Votua Reef were quantified using 30 X 2 m transects ( $n = 9$  transects area<sup>-1</sup>) that were non-overlapping and distributed haphazardly within the center of the of the shallow back-reef lagoon of each area. Within each transect, we located all *P. cylindrica* colonies that exceeded 25 cm in at least one horizontal dimension when a 25 X 25 cm grid was placed over the upper surface of the colony. Colonies were searched for *C. violacea* for  $\leq 6$  minutes (duration depending on colony size) and all snails were collected using needle-nose pliers and pooled for that site. Size of each snail was assessed as shell height (tip of the apex to the edge of the bottom lip) to the nearest 0.5 mm using a vernier caliper. To estimate *C. violacea* density per 2-dimensional area of coral, the upper surface of each coral colony was photographed, and surface area quantified via ImageJ.

Due to logistical constraints and the high abundance of *C. violacea* on colonies of *P. cylindrica* at Votua reef (1503 snails collected and measured), subsequent assessments of *C. violacea* density at Vatu-o-lalai and Namada reefs consisted of haphazardly surveying 20 *P. cylindrica* colonies near the center of each area, collecting snails and measuring shell height as described previously. Differences in *C. violacea* density between the MPA and fished area at each reef site were compared separately with ANOVA using a permutation approach (5000 permutations) in the R (v. 3.3.2) package lmpPerm (v. 2.1.0).

Differences in *C. violacea* size-frequency distributions between paired areas were assessed using Kolmogorov-Smirnov tests and represented with probability density histograms. Mean shell height of *C. violacea* were compared between paired MPAs and

fished areas with ANOVA using a permutation approach (5000 permutations) in the R (v. 3.3.2) package lmp (v. 2.1.0).

### ***Influence of C. violacea predation on coral growth and survivorship***

To investigate the effect of *C. violacea* feeding on the growth and survivorship of *P. cylindrica*, and how this varies with *C. violacea* size, we manipulated *C. violacea* feeding on replicate *P. cylindrica* branches outplanted in the field. In May 2016, four branches (6-8 cm in length; 18.1-55.3 g wet mass) were collected from 15 *P. cylindrica* colonies at Namuka Reef along the Coral Coast of Viti Levu, Fiji (18° 8'5.70"S, 177°23'14.94"E). Individual branches were embedded within the cut-off necks of inverted plastic bottles using epoxy (Emerkit) and their respective bottle caps were affixed to the substratum with a nail. This procedure allowed us to easily detach and reattach corals for periodic weighing with minimal disturbance (see Clements and Hay 2015, Clements et al. *in press* for methods). Following a ~1-month period of acclimation and recovery from fragmentation, corals were weighed in the field (see below) and then exposed to one of four treatments of *C. violacea* predation for 24 days: either (1) no snail (control), (2) one snail ~8 mm in height, (3) one snail ~15 mm in height, or (4) one snail ~22 mm in height. Height (i.e. tip of the apex to the edge of the bottom lip) of each snail was measured to the nearest 0.5 mm using a vernier caliper, and variance in shell height within a group was  $\pm 0.5$  mm. To ensure snails remained on their respective corals, we dried and sanded a small portion of each snail's shell, superglued a cable tie to the shell surface, and attached the tie around the base of each snail's *P. cylindrica* branch (Figure 4.2). Because these snails feed by staying in place at the base of a coral branch and consuming resources that the coral mobilizes to recover from feeding damage (Oren et al.

1998), this procedure mimicked natural feeding location and behavior seen in the field. After 24 days, corals were detached from the substratum and re-weighed in the field using an electronic scale (OHAUS Scout Pro) enclosed within a plastic container that was mounted to a tripod holding it above the water surface (as had been done for the initial weighing). Twenty-four to 48 hours before the weighing session, each coral's bottle-top/epoxy base was lightly brushed with a toothbrush to remove fouling organisms. Before weighing, each coral was gently shaken 30 times to remove excess water, and then weighed, immediately placed back into the water, and reattached to the substrate. Following weighing session, corals were separated from their epoxy base and each coral and base were weighed separately. This allowed the relative change in coral mass (as a percentage of initial mass) to be determined. Differences in percent mass change among corals exposed to different treatments were assessed using a one-factor ANOVA followed by a Tukey's post-hoc test.



Figure 4.2: Experimental set-up used to assess effects of *C. violacea* feeding on *P. cylindrica* growth and survivorship.



### ***Tethering experiments***

To investigate whether differences in *C. violacea* densities between MPAs and fished areas might be explained by differential rates of predation, we conducted a series of tethering experiments within the MPA and fished area at Votua Reef using *C. violacea* collected during density surveys. After drying and sanding a small patch on the surface of each shell, a ~6 cm length of monofilament line (0.14 mm, 6.9 kg test) was attached to each shell via super glue. Tethers were secured to the reef bottom using a U nail, with 10 snails at each of 10 locations separated by ~7-10 m within a network of interconnected pools near the center of the MPA and fished area. At each location, snails were divided into a group of smaller (4-14.5 mm) and larger (15-25 mm) shell height, both of which were either caged using 1-cm<sup>2</sup> grid metal screening (control) or left uncaged (treatment) ( $n = 5$  snails height<sup>-1</sup> treatment<sup>-1</sup> station<sup>-1</sup> area<sup>-1</sup>). *C. violacea* mortality was then monitored over 48 hrs. Data on percent mortality at 48 hrs were analyzed with ANOVA using a permutation approach (5000 permutations) in the R (v. 3.3.2) package *lmPerm* (v. 2.1.0) with snail location (MPA vs. fished), size (4-14.5 mm or 15-25 mm), and treatment (caged vs. uncaged) as fixed factors. Due to extensive hermit crab (*Calcinus* & *Dardanus* spp.) induced mortality on larger snails (15-25mm) (Figure 4.3), separate permutational ANOVA analyses were conducted to compare total mortality among treatments, as well as mortality due to hermit crabs (as evidenced by them occupying the shells) and mortality due to putative fish predators (i.e. snail shell partially or fully absent from the tether).

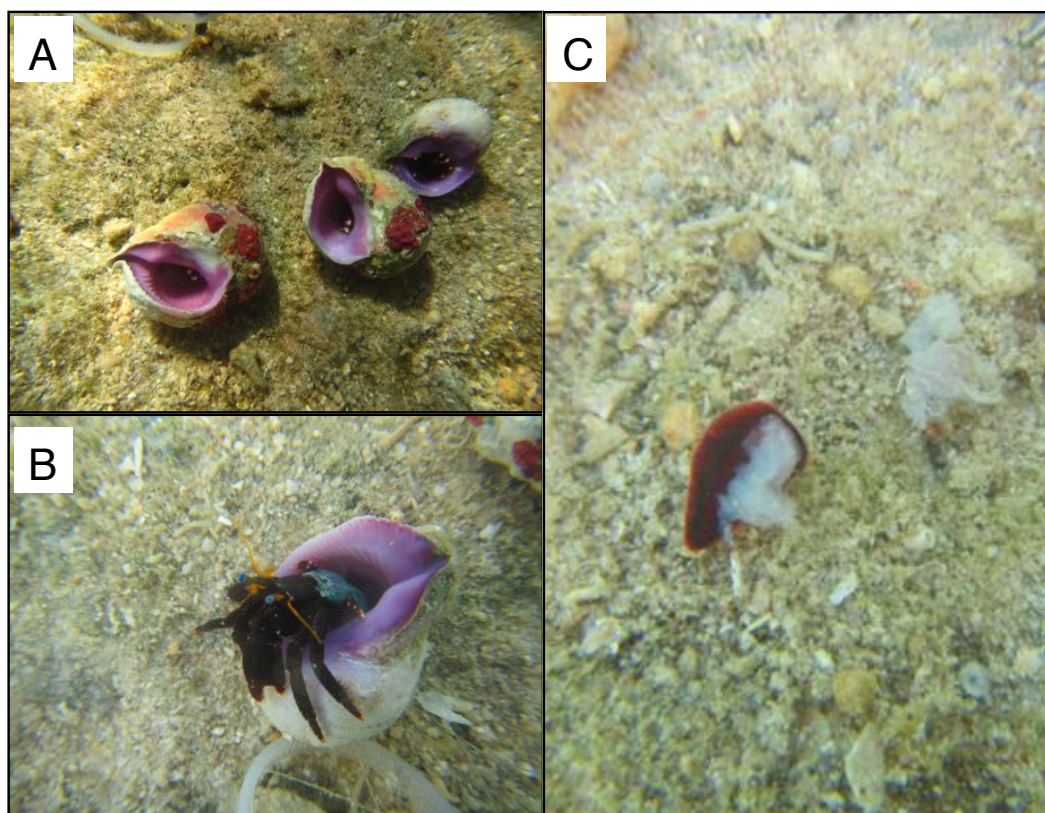


Figure 4.3: (A&B) Paguroid hermit crabs inhabiting shells of previously living *C. violacea* that were tethered to the benthos at Votua Reef ~24 h earlier. (C) Remnants of tissue and the operculum of *C. violacea* at the tethering location.

To simulate more ecologically relevant predation scenarios and possibly reduce predation by hermit crabs, we subsequently conducted a tethering experiment where three *C. violacea*, 4-9 mm in shell height, were tethered to small colonies of *P. cylindrica* that had been previously implanted within the cut-off necks of inverted plastic bottles using epoxy (Figure 4.4). Snails were first attached to monofilament in the same manner as described above. The monofilament was then attached to a cable tie, which was secured to the cut-off bottleneck containing an individual coral (3 snails coral<sup>-1</sup>). Each bottle portion and respective coral was then screwed into a bottle cap embedded within the substrate near-shore in Votua Reef's MPA and surrounded by 1-cm<sup>2</sup> grid metal screening. Corals and tethered snails were held within cages ~48 hrs to allow snails to attach to the corals, after which each coral was then deployed into a bottle cap embedded within the substrate of either the MPA or fished areas at each of the 10 stations used in the prior tethering experiment. At each station, this included an uncaged *P. cylindrica* and a caged control surrounded by 1-cm<sup>2</sup> grid metal screening ( $n = 10$  corals treatment<sup>-1</sup> area<sup>-1</sup>). *C. violacea* mortality was then monitored over 72 hrs. Caged controls did not exhibit any snail mortality, and were therefore excluded from subsequent analyses. Percent mortality data of uncaged snails from the MPA and fished area were compared with ANOVA using a permutation approach (5000 permutations) in the R (v. 3.3.2) package lmpPerm (v. 2.1.0).

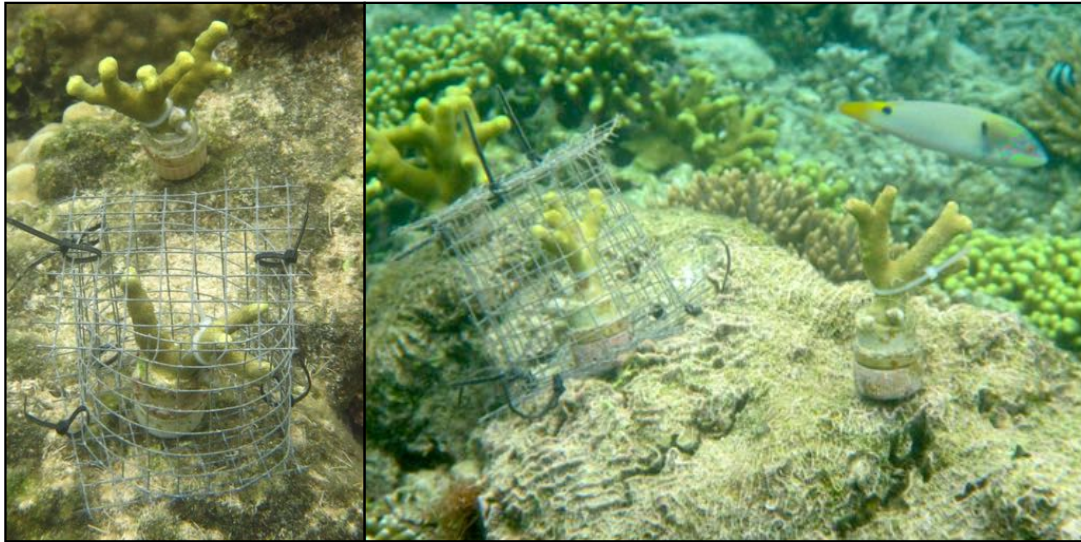


Figure 4.4: Manipulations used in tethering experiment to assess the impact of predation on *C. violacea* within the MPA and fished area at Votua Reef.

## Results

*C. violacea* densities were ~4-35 times greater on *P. cylindrica* colonies within fished areas (~8-12 individuals 1000 cm<sup>-2</sup>) versus MPAs (~0.3-3 individuals 1000 cm<sup>-2</sup>) ( $p < 0.001$ , Figure 4.5), with snails from MPAs being significantly larger ( $p \leq 0.014$ ) and exhibiting different size-frequency distributions ( $p \leq 0.03$ ) than snails from paired fished areas (Figure 4.6).

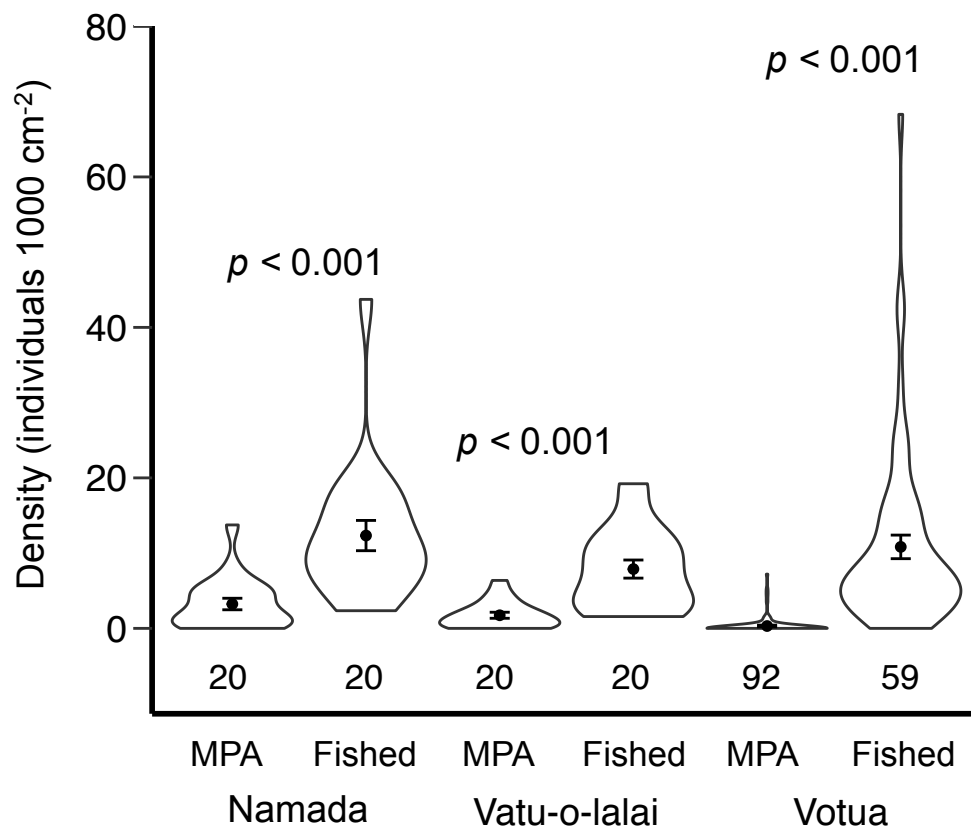


Figure 4.5: Violin plots depicting mean  $\pm$  SE *C. violacea* densities (black dots and error bars) on *P. cylindrica* colonies within MPAs and adjacent fished areas at each village site. Numbers below individual violin plots indicate number of *P. cylindrica* colonies surveyed. Data for each pairwise comparison were analyzed with ANOVA using a permutation approach (5000 permutations).

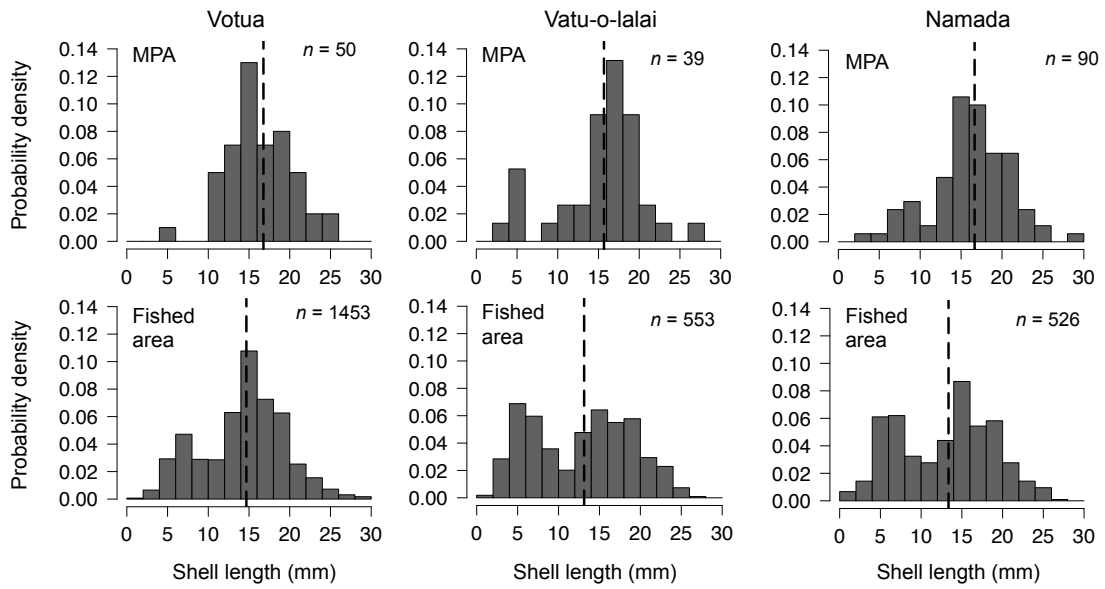


Figure 4.6: Density histograms representing of *C. violacea* size-frequency distributions within MPAs and fished areas at Votua, Vatu-o-lalai, and Namada Reefs. Dashed black lines denote mean *C. violacea* shell length (mm) for each area. Number of *C. violacea* assessed are indicated in the upper right corner of each histogram.

When feeding on corals in the field, *C. violacea* significantly reduced *P. cylindrica* growth compared to corals not hosting gastropods (ANOVA:  $F_{3,57} = 34.0883$ ,  $p < 0.001$ ), with suppression of coral growth being a function of snail size (Figure 4.7). Twenty-two mm *C. violacea* reduced growth by 43%, 15 mm snails by 25%, and 8 mm snails by 18%. No corals died during the 24-day experiment.

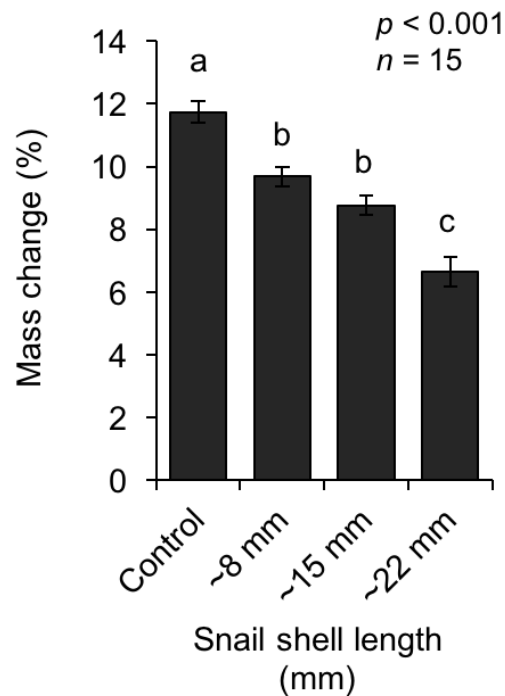


Figure 4.7: Percentage change in mass of *P. cylindrica* corals exposed to feeding by different-sized *C. violacea* for 24 days. Letters above the bars represent significant groupings from a one factor ANOVA followed by Tukey's post-hoc test.



After 48 hours tethered on the benthos, snails of 15-25 mm in height suffered significantly greater mortality (72-94%) than snails 4-14.5 mm in height (8-28%) ( $p < 0.001$ , Figure 4.8), regardless of location (MPA or fished area;  $p = 0.282$ ) or caging status (caged or uncaged;  $p = 0.114$ ). The high frequency with which hermit crabs occupied the tethered shells indicated that 15-25 mm snails suffered greater hermit crab-induced mortality, regardless of location ( $p = 0.051$ ) or caging status ( $p = 0.081$ ), than 4-14 mm snails ( $p < 0.001$ , Figure 4.8B). Placing hermit crabs and larger snails together in the lab also demonstrated that crabs were actively killing gastropods and moving into their shells – usually within 6-8 hrs of initial contact (C. Clements, personal observation). Caging did significantly affect the probability of snails being completely missing from their tether ( $p < 0.001$ ) – presumably due to fish predation. But for this group, differences in mortality due to snail size ( $p = 0.482$ ) and location ( $p = 0.130$ ) were not significant (Figure 4.8C). When tethered to *P. cylindrica* corals (instead of on the substrate) for 72h in the field, small (4-9 mm in height) *C. violacea* experienced ~220% greater mortality (i.e. removal from tether) in the MPA than the fished area ( $p = 0.034$ , Figure 4.9), presumably due to predation by fishes as evidenced by shell crushing and fragments remaining near the tethering site (Figure S4).

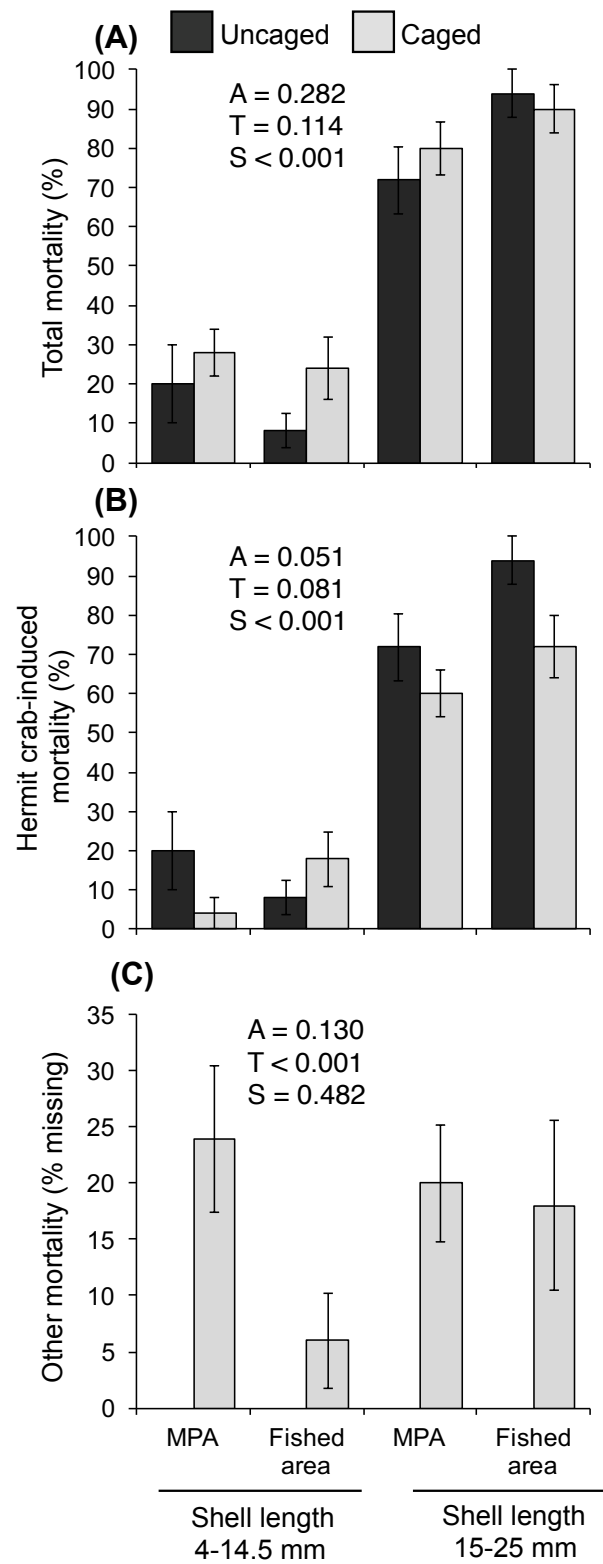


Figure 4.8: Percent total mortality (A), and the % due to hermit-crabs (B) versus other mortality (C) (mean  $\pm$  SE) of caged (black bars) and uncaged (gray bars) *C. violacea* of varying size during a 48 hr tethering experiment on the benthos within Votua reef's MPA and fished area. Five snails of each size class (4-14.5 mm or 15-25 mm) were tethered at each of 10 locations within each habitat type. Data were analyzed with ANOVA using a permutation approach (5000 iterations). *P*-values for fixed terms from these analyses are presented in the upper right of each figure. A = area (MPA or fished area); T = caging treatment (uncaged or caged); S = shell length (4-14.5 mm or 15-25mm).

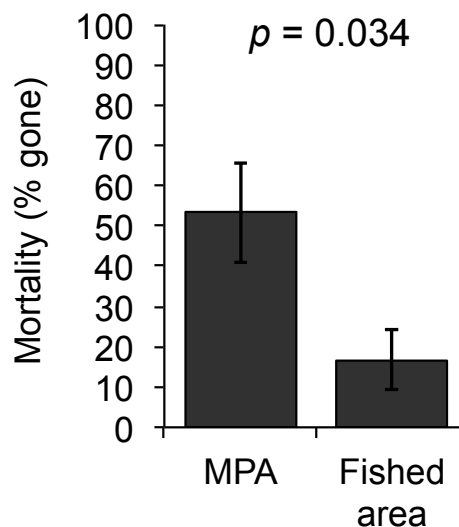


Figure 4.9: Mortality (% mean  $\pm$  SE) over 72h of uncaged *C. violacea* (4-9 mm shell length) when tethered on *P. cylindrica* branches within Votua Reef's MPA and fished area. Three snails with shell lengths 4-9 mm were tethered to each coral ( $n = 10$  corals area<sup>-1</sup>). Data were analyzed with ANOVA using a permutation approach (5000 iterations).

## Discussion

As corals decline and coral stressors increase (Hoegh-Guldberg et al. 2007, Carpenter et al. 2008, Hughes et al. 2017), predation on the lower number of surviving corals may be especially important (Knowlton et al. 1990). This may occur even for low metabolic rate, “prudent predators,” like snails (Oren et al. 1998), whose impacts were previously considered minor to negligible; even these consumers can appreciably affect the persistence, recovery, and management of remaining corals (Burkepile and Hay 2007, Rotjan and Lewis 2008, Cole et al. 2011, Cole and Pratchett 2011). We found that predation by the corallivorous gastropod *C. violacea* reduced growth of *P. cylindrica* by 18-43% (depending on snail size) over a period of only 24 days. This coral is common on degraded reefs in Fiji and elsewhere (McClanahan and Mutere 1994) and is commonly one of the last abundant survivors on stressed reefs due to its reduced sensitivity to a number of stressors associated with coral decline (Pratchett 2010, Rasher et al. 2011, Bonaldo and Hay 2014). *C. violacea* densities were up to 35x greater on *P. cylindrica* colonies within fished areas than within paired MPAs. Furthermore, *C. violacea* height-frequency distributions in MPAs vs. fished areas, as well as *C. violacea* mortality data from tethering experiments, suggest that these small MPAs were likely fostering trophic interactions that suppress *C. violacea* numbers, especially the smaller, recently recruited juveniles. A comparison of size distributions within MPAs and fished areas (Figure 4.6) suggests that younger age/size cohorts are persisting in the fished areas but being suppressed within the MPAs.

*C. violacea* is a sessile predator that utilizes a ‘prudent’ mode of feeding, whereby the snail inserts its proboscis into the coral polyp’s coelenteron and feeds as the coral

translocates resources to replace those being consumed (Oren et al. 1998). Visually, *C. violacea* predation results in only small and localized tissue damage; this may have contributed to this consumer being overlooked as an ecologically important coral predator. However, their feeding can considerably suppress growth (Figure 4.7), is associated with secondary colonization by competitors and pathogens such as algae and fungi (Raymundo et al. 2016), and may also weaken corals that then experience increased mortality when exposed to other stressors such as ocean warming (L. Shaver personal communication). *C. violacea* feeding did not affect mortality over the course of our study, but feeding by a single individual reduced *P. cylindrica* growth ~18-43%, depending on snail size. In our field surveys, we observed *P. cylindrica* colonies with *C. violacea* densities of up to 68 snails per 1000 cm<sup>2</sup> and at least one large colony (surface area = 1.2 m<sup>2</sup>) hosted >200 snails (see Figure 4.10). Such densities may reduce colony growth substantially and impose growth-related opportunity costs that undermine coral fitness and resilience (e.g. increased mortality risk, and decreased competitive ability and fecundity) (Hall and Hughes 1996, Zilberberg and Edmunds 2001, Edmunds and Gates 2004), especially for corals dealing with other stressors common to degraded reefs (e.g. macroalgal competition [McCook et al. 2001, Clements et al. 2017], disease [Raymundo et al. 2009, Nicolet et al. 2013, Katz et al. 2014], and physical stresses [Knowlton et al. 1990]).

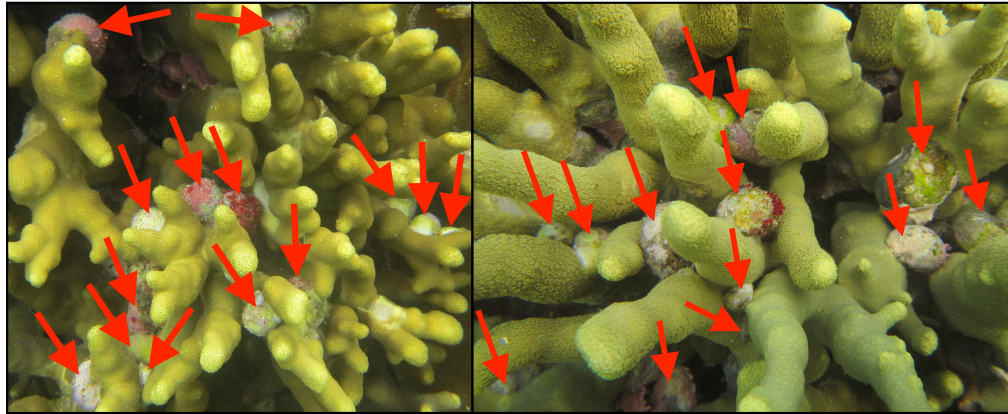


Figure 4.10: Examples of natural *C. violacea* densities on *P. cylindrica* colonies in the field. Red arrows are pointing to *C. violacea* actively feeding on *P. cylindrica*.

Our field surveys indicated that *C. violacea* densities were significantly reduced on *P. cylindrica* colonies within the MPAs compared to adjacent fished areas. Previous studies conducted along the coast of Kenya documented reduced densities of corallivorous gastropods, particularly *C. violacea*, in protected areas compared to neighboring fished areas (McClanahan 1989, 2002). However, unlike the Kenyan MPAs that are tens to hundreds of square kilometers in size, the Fijian MPAs that we surveyed are small community-managed initiatives ranging from 0.45-0.78 km<sup>2</sup> in total area. Our findings add to a growing body of evidence highlighting the utility of small MPAs (Russ and Alcala 1996, Halpern 2003, Clements et al. 2012, Bonaldo et al. 2017, Espectato et al. 2017), which are increasingly the primary tool used for management of coastal marine resources across the Pacific (Jupiter et al. 2014).

Based on correlative evidence, McClanahan (1994) hypothesized that predatory fishes, particularly labrids and balistids, were suppressing *C. violacea* abundance in Kenyan MPAs compared to fished areas. Height-frequency distributions of *C. violacea* collected during our surveys, coupled with evidence from our tethering experiments, suggest that predation also is driving differences in *C. violacea* densities and size distributions between the paired MPAs and fished areas we studied. Mean shell heights of *C. violacea* were greater at all three MPAs compared to their respective fished areas, likely due to the relatively low frequency of smaller size classes of *C. violacea* observed in the MPAs. Evidence from our tethering experiment indicated that these differences may be due to increased fish predation on smaller *C. violacea*. These snails feed without moving for extended periods of time, a strategy hypothesized to help them evade ‘tracking’ by predatory fishes via exposure of white coral skeleton during feeding

(Kitting 1975).

When we tethered small (4-9 mm) snails to *P. cylindrica* (their normal place of occurrence) in Votua's MPA and fished area, loss of snails over 72h was 220% greater in the MPA than the fished area. We did not identify specific predators of *C. violacea*, but shell remnants found within the immediate vicinity (< 30 cm) of the tethering locations suggests that predation was likely by shell crushing fishes (e.g. balistids, labrids, tetradontids, etc.) (Figure 4.11). Predators of both invertebrates and fishes are more abundant in the MPAs versus the fished areas of our study reefs (Clements et al. 2012, Bonaldo et al. 2017). In contrast to the heavy predation on small snails when in their natural position on their host, we found less conclusive results when snails were tethered on open substrate on the benthos. In this situation, differences in total mortality for smaller snails (4-14.5 mm) were not significant between sites (MPA vs. fished area) or treatments (caged vs. uncaged), but appeared to be trending towards greater mortality in the MPA when considering only individuals completely removed from their tether (as opposed to being removed from their shell by a hermit crab). Hermit crab-induced mortality on larger shells in this size class (13-14.5 mm) may have also obscured our ability to adequately assess mortality via fish predation in this case.



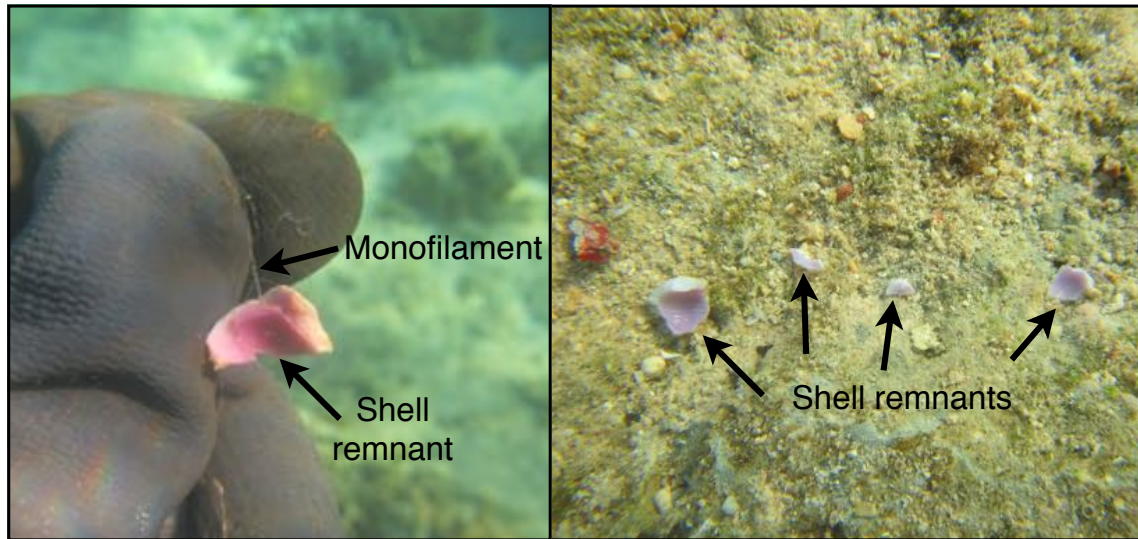


Figure 4.11: Remnants of a *C. violacea* shell previously tethered to *P. cylindrica* within Votua Reef's MPA.

Differences in total mortality for larger snails (height = 15-25 mm) were not significant between the MPA and fished area or between caged and uncaged individuals. The dominant source of mortality (60-95%) among individuals of this size class was hermit crabs that physically removed snails to occupy their shell (C. Clements personal observation, Figure 4.3). Caging did not exclude hermit crabs, allowing hermit crab-induced mortality to be equivalent between caged and uncaged snails, for both size classes (4-14.5 mm & 15-25 mm). Although recent laboratory experiments have questioned whether hermit crabs can remove live snails from their shells (Laidre 2011), we commonly observed our previously live snails being occupied by hermit crabs after 48h, and with the shells undamaged. Additionally, when we placed snails and hermit crabs together in containers in the lab, hermit crabs did kill snails and occupy their shells, often within only a few hours (C. Clements personal observation). This crab predation of snails does not appear to be an anomaly of our study site; similar anecdotal cases have been reported in the literature (Brichtwell 1951, Randall 1964, Rutherford 1977, Iversen et al. 1986) and may be expected due to strong competition for limited shell resources (Kellogg 1976, Bertness 1981). The prudent sessile feeding utilized by *C. violacea* (Oren et al. 1998), may have been in part selected for as a means of preventing the need to move among hosts, as movement among hosts is obviously dangerous at our study site (Figure 4.8), as well as for gastropods in other systems where occupying hosts provides relative safety but moving across the benthos to new hosts entails high risks of predation (Schmitt et al. 1983).

Impacts of corallivores that were once considered negligible are increasingly being reconsidered (Cole et al. 2011) as reefs further degrade and managers try to build

resilience among remaining corals in the face of a global change (Hughes et al. 2010).

Our study highlights the relatively overlooked impacts that *C. violacea* can have on coral growth, which will reduce coral fitness and resilience to other stressors, contributing to reef degradation. This could be especially problematic for corals after bleaching events or other disturbances that suppress coral densities but leave snails at high densities and in need of food. Even the small MPAs investigated here suppressed *C. violacea* densities and presumably their impact on this important stress-tolerant coral.

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## **Chapter 5**

### **BIODIVERSITY ENHANCES CORAL GROWTH, SURVIVORSHIP, AND RESISTANCE TO COMPETITORS**

#### **Abstract**

Coral reefs are in global decline, losing both coral cover and diversity. Here we manipulated coral species richness in field experiments to assess the role of coral diversity in affecting coral growth and survival. Conspecific corals exhibited up to 190% greater growth and 40% less tissue mortality in multispecies compared to single-species plots; macroalgal competitors of corals also were more successful in some single-species plots. Total coral growth in polyculture was greater than (at four months) or equal to (at sixteen months) total growth in the most productive monoculture, suggesting that both selection and complementarity effects enhanced coral community performance. Our findings highlight the positive role of biodiversity in coral reef ecosystem function, and have worrisome implications for coral resistance and resilience to increasing disturbances.

#### **Introduction**

Understanding the role of biodiversity in ecosystem function becomes increasingly critical as natural communities are simplified or homogenized by extinctions, invasions, and a host of other pressures (Naeem et al. 2012). This may be especially critical on coral reefs, which are normally complex and biodiverse, but are now becoming degraded and species poor (Bellwood et al. 2004, Mumby and Steneck 2008). If we are losing both species and critical interactions that depend on biodiversity, then species loss in diverse systems like tropical reefs may initiate negative feedbacks (a

biodiversity melt-down) that suppress resilience, recovery, and exacerbate losses of both biodiversity and ecosystem function. Species loss is now considered among the most serious threats to ecosystem function and integrity (Hooper et al. 2012); this can occur due to loss of keystone or foundation species, but may also occur due to loss of positive interactions among potential competitors (Naeem et al. 2012).

The function and maintenance of coral species diversity in reef ecosystems has long intrigued ecologists (Connell 1978), yet few experimental tests of biodiversity-ecosystem function have been conducted on coral reefs. The diversity of corals and coral-associated species on tropical reefs is phenomenal, but these ecosystems are in dramatic decline with reefs worldwide converting from species-rich communities dominated by corals to lower diversity communities dominated by seaweeds (Hughes et al. 2010). Coral losses are accelerating due to increasing global stressors (Hoegh-Guldberg et al. 2007, Hughes et al. 2017), generating an urgent need to understand how coral diversity influences ecosystem processes. Investigations to date have focused on relationships between coral and fish species richness (Messmer et al. 2011, Holbrook et al. 2015) not the impacts of coral diversity on corals. Studies of the latter are limited to large-scale correlative analyses yielding mixed results (Zhang et al. 2014). Manipulative experiments assessing ecosystem performance (e.g., production, invasion resistance) for coral species in single vs. multispecies settings are lacking, despite corals being the foundation taxa upon which most reef species depend.

In this field study, we created experimental monocultures and polycultures of three common Indo-Pacific coral species (*Porites cylindrica*, *Pocillopora damicornis*, and *Acropora millepora*) to test effects of coral species richness on coral growth,

mortality, and colonization by competing macroalgae – three key measures of reef ecosystem function.

## **Materials and Methods**

### ***Study site and organisms***

Our study was conducted from December 2014 to April 2016 on a ~1-3 m deep back-reef lagoon at Votua Village, Viti Levu, Fiji (18°12'46.13"S, 177°42'15.61"E) that is subjected to artisanal fishing and exhibits low coral cover (~5%) and high macroalgal cover (~91%) (Rasher et al. 2013). Our manipulative experiment used the corals *Porites cylindrica*, *Pocillopora damicornis*, and *Acropora millepora*; three species common on reefs throughout the Indo-Pacific and on the reef where we conducted our study, as well as on adjacent protected areas that were coral, instead of macroalgal, dominated (Bonaldo and Hay 2014). These species were chosen due to their local abundance and because they are representative of coral families that differ in their reproductive strategies (Baird et al. 2009), growth rates (Darling et al. 2012), and vulnerability to disturbances such as macroalgal allelopathy (Rasher and Hay 2010, Rasher et al. 2011), bleaching (Loya et al. 2001, Bonaldo and Hay 2014), and *Acanthaster* spp. predation (Pratchett 2007, Kayal et al. 2012).

### ***Coral performance in monocultures vs. polycultures***

To manipulate coral species composition and richness, we created 36 x 36 x 6 cm cement plots to serve as the substrate for replicate monoculture and polyculture coral communities. Each plot was attached to a concrete block (19 x 9 x 19 cm) affixed to the reef bottom near the center of the shallow (1-3 m) back-reef lagoon. This elevated plots 25 cm above the bottom and minimized damage associated with the benthos during

storms (e.g. sand scour, burial by unconsolidated rubble, crushing by dislodged coral heads, etc.). This elevation mimicked positioning of many natural coral colonies, which often occurred on small bommies that elevated them above the reef pavement to which our plots were anchored. The upper surface of each plot consisted of a 6 x 6 cm grid, and in every other grid space, the outer surface of a soda bottle cap was embedded flush with the plot's upper surface (18 bottle caps per plot). Similar sized-branches (6-8 cm in length) of *P. cylindrica*, *P. damicornis*, and *A. millepora* corals were collected from colonies across the lagoon (18 colonies per species) and were individually epoxied (Emerkit epoxy) into the cut-off necks of plastic soda bottles during late December 2014. These inverted soda bottle necks and corals could then be anchored into the plot by screwing each into its designated bottle cap embedded within the plot. To assemble monocultures of each species, eighteen conspecifics collected from different colonies were randomly embedded within each plot ( $n = 12$  plots per monoculture, 216 corals per species in monoculture plots). To assemble polycultures, six individuals of each species from different colonies were embedded in the same manner at randomized locations within each plot ( $n = 12$  plots, 72 corals per species) (Figure 5.1). Overall, the experiment involved 864 individual corals – 288 per species embedded within either monoculture or polyculture plots.

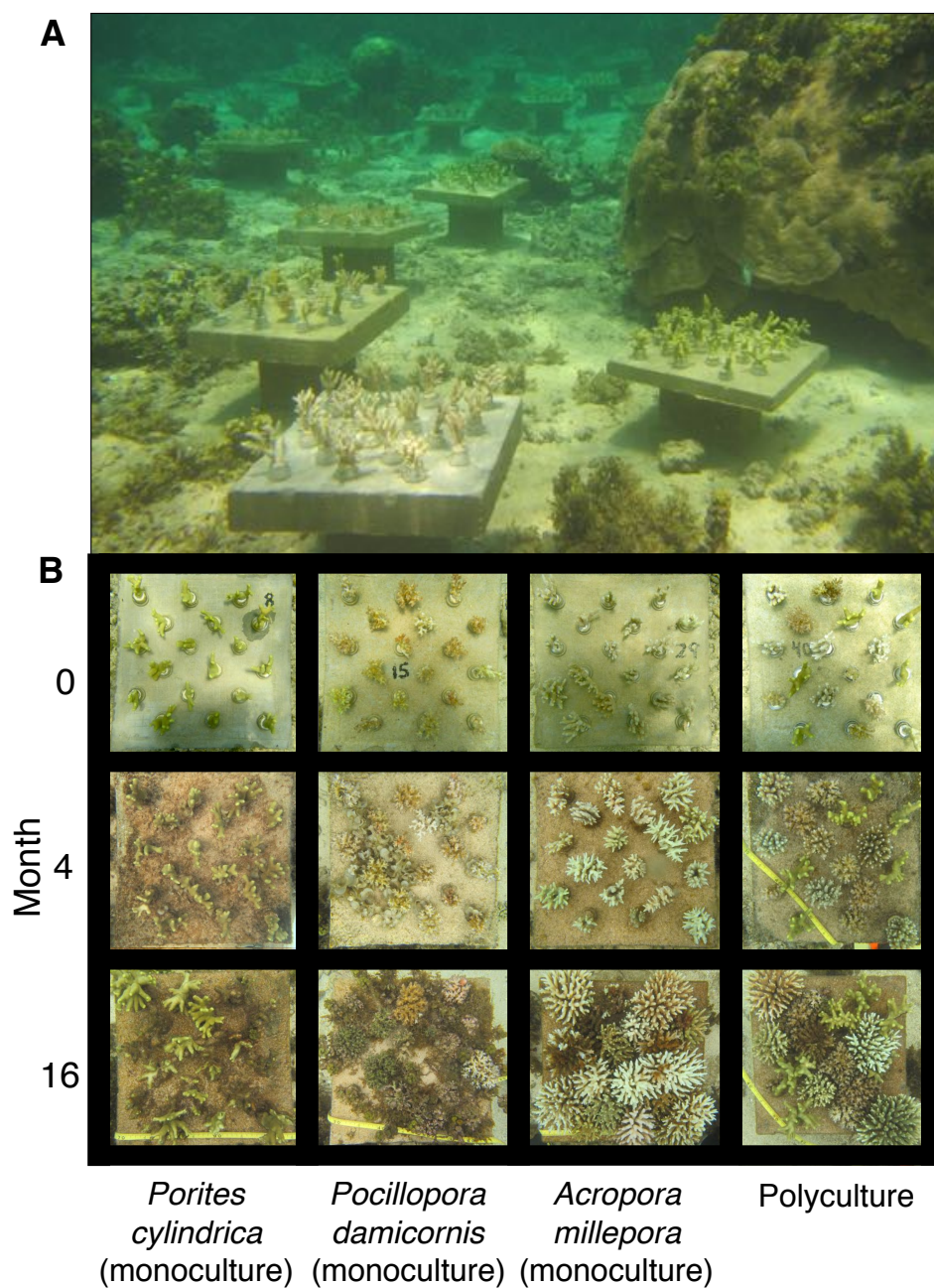


Figure 5.1: Coral monoculture and polyculture plots used in the experiment. (a) Monoculture and polyculture plots at the beginning of the experiment (month zero). (b) Monocultures of *Porites cylindrica* (far left), *Pocillopora damicornis* (center left), and *Acropora millepora* (center right), and a polyculture containing all three species (far right) at zero (top), four (middle), sixteen (bottom) months.

Percent growth and tissue mortality of individual corals in each plot, as well as colonization of each plot by benthic macroalgae, were assessed at four and sixteen months (April 2015 and 2016, respectively). We visually estimated percent tissue mortality of each coral fragment in the field. To assess coral growth, corals and their epoxy/bottle top base were wet-weighed in the field using an electronic scale (OHAUS Scout Pro) enclosed within a plastic container mounted to a tripod holding it above the water surface. Twenty-four to forty-eight hours before weighing sessions, each coral's bottle-top/epoxy base was brushed clean of fouling organisms. Before weighing, each coral was gently shaken thirty times to remove excess water, weighed, immediately placed back into the water, and reattached to its respective bottle cap. At the end of the experiment (16 months), each coral was separated from its bottle-top/epoxy base, and each coral and base were weighed separately. We could then determine, via subtraction, coral mass and thus percent growth throughout the experimental period. To assess plot colonization by benthic macroalgae at 4 months, photographs of each plot were analyzed for the percentage cover of macroalgae using ImageJ (v. 1.8.0\_121). At 16 months, we assessed macroalgal abundance by manually collecting all upright macroalgae from the upper surface of each plot, separating to genus, and wet-weighing after removing excess water using a salad spinner (15 revolutions per sample).

### ***Statistical analyses***

We used linear mixed effects (LME) models in the R (v. 3.3.2) package nlme (v. 3.1-130) to assess differences in percent mass change at both four and sixteen months between conspecific corals in monocultures and polycultures. We also compared the combined percent mass change of all species in polyculture to that of all species in

monoculture, as well as percent mass change of corals in polycultures compared to the most productive monoculture (i.e. *Acropora millepora*). Individual corals within plots that had been completely broken off from their bottle top base were excluded from analyses; this occurred to only 23 of our 864 corals (2.6%) at four months and 143 corals at sixteen months (16.6%), did not vary significantly with treatment ( $p \geq 0.478$ ; permutation ANOVA (5000 permutations)), and in some observed instances was due to human trampling. Models were fitted using restricted maximum likelihood with plot type (i.e., monoculture & polyculture) as a fixed factor and individual replicate plots treated as a random effect nested within plot type. When individual models did not meet assumptions of homogenous variance and normally distributed errors, we reran the analysis and specified the variance structure using the varIdent function in nlme.

To assess differences in percent tissue mortality at four and sixteen months between conspecific corals in monocultures vs. polycultures, we first averaged percent tissue mortality of individual corals in each plot. Mean tissue mortality of conspecifics in monoculture and polyculture plots at each time point were then compared separately with ANOVA using a permutation approach (5000 permutations) in the R (v. 3.3.2) package lmPerm (v. 2.1.0). Macroalgal colonization of polycultures and monocultures of each species at four and sixteen months were compared separately with ANOVA and Tukey post-hoc tests using a permutation approach (5000 permutations) in the R (v. 3.3.2) package lmPerm (v. 2.1.0).



## Results

### ***Coral growth in monocultures vs. polycultures***

At four months, percent coral growth was greater for *Porites* (+27%,  $p = 0.018$ , LME), *Pocillopora* (+185%,  $p < 0.001$ , LME), and *Acropora* (+21%,  $p = 0.047$ , LME) when grown in polyculture compared to monoculture (Figure 5.2a). The combined growth of all three species in polyculture was ~61% greater than the combined growth of all three species in monoculture ( $p < 0.001$ , LME; Figure 5.2b) and ~24% ( $p = 0.016$ , LME) greater than the best performing (*Acropora*) monoculture (Figure 5.2c). At sixteen months, percent growth was significantly greater for *Porites* (+74%,  $p = 0.016$ , LME) and *Pocillopora* (+191%,  $p < 0.001$ , LME) in polyculture compared to conspecifics in monoculture, but this pattern was no longer significant for *Acropora* (+23%,  $p = 0.231$ , LME; Figure 5.2d). The combined growth of all three species in polyculture was again greater than the combined growth of all three species in monoculture (+67%,  $p < 0.001$ , LME; Figure 5.2e), but was statistically indistinguishable (-13%,  $p = 0.377$ , LME) from the best performing (*Acropora*) monoculture (Figure 5.2f).

### ***Coral tissue mortality in monocultures vs. polycultures***

Coral tissue mortality at four months was not significantly different between conspecifics of *Porites* ( $p = 0.167$ , permutation ANOVA) and *Acropora* ( $p = 0.745$ , permutation ANOVA) grown in polyculture vs. monoculture (Figure 5.3a), but *Pocillopora* in monoculture exhibited ~218% more tissue mortality than conspecifics in polyculture ( $p = 0.016$ , permutation ANOVA). At sixteen months, *Pocillopora* and *Porites* in monoculture had 90% ( $p = 0.016$ , permutation ANOVA) and 105% ( $p = 0.007$ , permutation ANOVA) greater tissue mortality, respectively, than conspecifics in

polyculture, but *Acropora* tissue mortality was comparable between conspecifics in polyculture and monoculture ( $p = 0.448$ , permutation ANOVA) (Figure 5.3b).

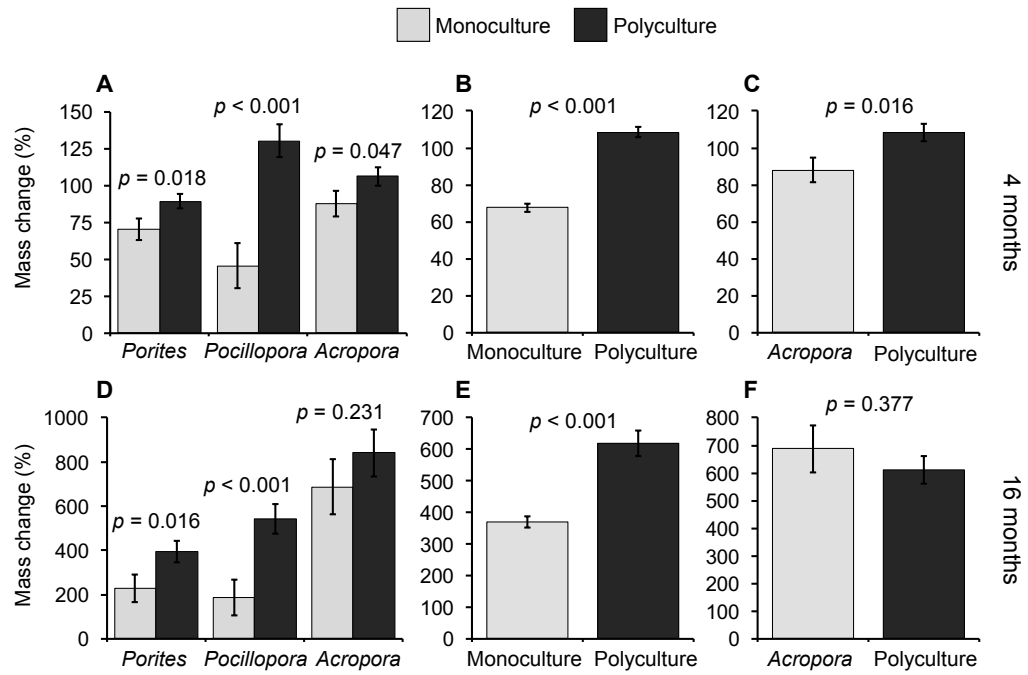


Figure 5.2: Coral growth is often enhanced in polyculture vs. monocultures. Coral growth (mean %  $\pm$  SE) at four months for: (A) *Porites cylindrica*, *Pocillopora damicornis*, and *Acropora millepora* in monocultures vs. polycultures, (B) the combined growth of *Porites*, *Pocillopora*, and *Acropora* in monocultures vs. polycultures, (C) *Acropora millepora* (the best performing monoculture) vs. the combined change of *Porites*, *Pocillopora*, and *Acropora* in polycultures. (D), (E), and (F) mirror A, B, and C, but at sixteen months.  $p$ -values from linear mixed effect models.

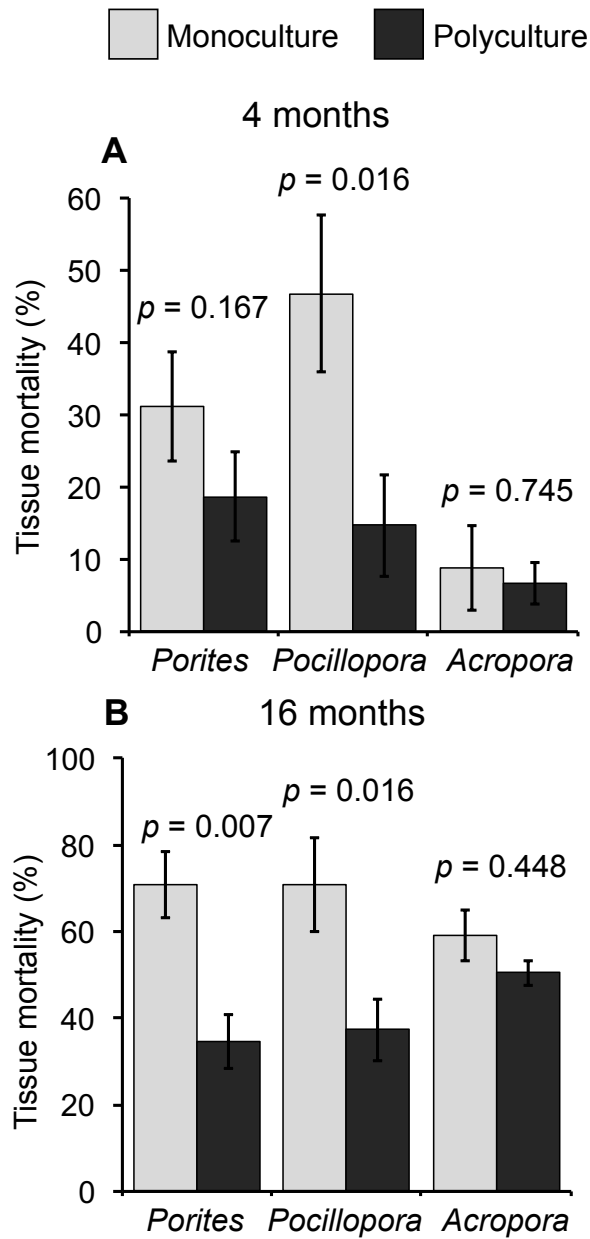


Figure 5.3: Coral tissue mortality in polyculture vs. monoculture. (A) Percent tissue mortality (mean %  $\pm$  SE) at four months for *Porites cylindrica*, *Pocillopora damicornis*, and *Acropora millepora* in monocultures vs. polycultures. (B) As above, but at sixteen

months.  $p$ -values from ANOVA using a permutation approach (5000 permutations).

### ***Macroalgal colonization in monocultures vs. polycultures***

At four months, macroalgal cover was significantly greater in *Pocillopora* monoculture than in all other treatments (Figure 5.4a). This general pattern remained at sixteen months; macroalgal biomass in *Pocillopora* monoculture was 6.1-6.4 times greater than polyculture ( $p = 0.024$ , permutation ANOVA) and *Acropora* monoculture ( $p = 0.025$ , permutation ANOVA), but was not significantly different than *Porites* monoculture ( $p = 0.110$ , permutation ANOVA), though the trend was suggestive (Figure 5.4b). All other post-hoc pairwise comparisons were nonsignificant.

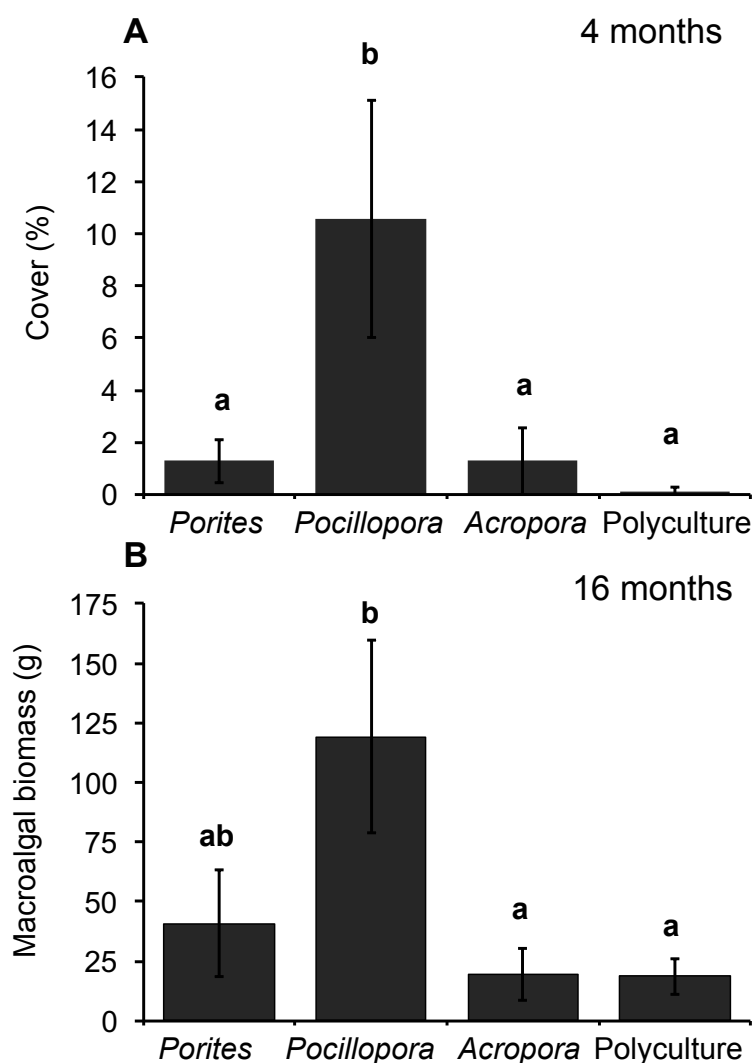


Figure 5.4: Macroalgal colonization in monoculture vs. polyculture plots. (A) Percent cover of upright macroalgae (mean  $\pm$  SE) at four months and (B) biomass of upright macroalgae at sixteen months for monocultures of *Porites cylindrica*, *Pocillopora damicornis*, and *Acropora millepora* and polycultures containing all three species. Letters indicate significant groupings ( $p < 0.05$ ) via ANOVA and Tukey post-hoc tests using a permutation approach (5000 permutations).

## Discussion

In early stages of the experiment, we consistently found a *richness effect* (*sensu* Stachowicz et al. 2007). At four months; all three coral species had a significant growth advantage (21-185%) when in polyculture vs. monocultures (Figure 5.2A). When summed across monocultures, change in coral mass was 61% greater in polyculture than in monocultures (Figure 5.2B), and 24% greater than the best performing monoculture (i.e. *A. millepora*; Figure 5.2C). At sixteen months, growth of *P. cylindrica* and *P. damicornis* was a significant 74% and 190% greater, respectively, in polyculture vs. monocultures, while growth of *A. millepora* no longer differed significantly between polyculture vs. monoculture (Figure 5.2D). Coral growth in polyculture also no longer exceeded that of the best performing monoculture (*A. millepora*; Figure 5.2F). However, total coral growth in polyculture still exceeded growth averaged across all monocultures by a significant 67% (Figure 5.2E). Differential growth may be attributable to enhanced mortality in monoculture vs. polyculture. At four months, tissue mortality was 219% greater for *P. damicornis* in monoculture vs. polyculture and trended that way for *P. cylindrica* (Figure 5.3A). At sixteen months, tissue mortality was a significant 90% and 74% greater for *P. damicornis* and *P. cylindrica*, respectively, when in monoculture vs. polyculture (Figure 5.3B). *A. millepora* tissue mortality was unaffected by treatment. The rapid and high (40%+) tissue mortality of *P. damicornis* in monoculture was associated with increased abundance of macroalgal competitors at both four and sixteen months (Figure 5.4). By sixteen months, *P. cylindrica* was exhibiting a similar, but non-significant, trend.

Richness effects can occur via (i) complementarity effects among species such as

resource partitioning or facilitation, or (ii) selection effects involving the inclusion of a species with a disproportionately large impact on the metric of interest (Hooper et al. 2005, Stachowicz et al. 2007, Hector and Wilby 2009). We found evidence for both. At four months, growth of all coral species in polyculture exceeded the best performing monoculture (*A. millepora*), an example of transgressive overyielding and indicative of complementarity (Hooper et al. 2005). However, by sixteen months, growth of *A. millepora* in monoculture no longer differed from the combined growth of all species in polyculture, suggesting that inclusion of the fast-growing Acroporid (Dullo 2005) likely contributed to rapid growth of polycultures (i.e. selection effect). Both complementarity and selection effects may occur, but may change with community age.

Differences in coral growth between polyculture vs. monocultures were likely affected by among-treatment differences in tissue mortality. *P. damicornis* experienced significantly greater tissue mortality in monoculture compared to polyculture at both four and sixteen months, while *P. cylindrica* showed a trend at four months that became significant by sixteen months (Figure 5.3). All coral species exhibited significant negative relationships between growth and tissue mortality (Figure 5.5), with the strength of this being greater for *P. damicornis* and *P. cylindrica* than for *A. millepora*. The strength of these relationships increased across time for *P. damicornis* and *P. cylindrica* but not for *A. millepora*. *P. damicornis* monocultures experienced considerable partial and whole coral mortality within only four months, likely contributing to enhanced macroalgal colonization within these plots (Nugues and Bak 2006). In contrast, *A. millepora* experienced limited tissue mortality (< 10%) at four months that was statistically indistinguishable between polyculture and monoculture (Figure 5.3a). This

low rate of *A. millepora* mortality likely contributed to coral growth, rapid monopolization of space (see Figure 5.1), and limited opportunity for macroalgal colonization. At sixteen months, *A. millepora* mortality in polyculture and monoculture had increased to 50% and 59%, respectively, but this appeared to be due to a February 2016 bleaching event (Hughes et al. 2017) after corals had grown considerably (Figure 5.6). This late stage mortality likely explains the weak relationship between *A. millepora* growth and tissue mortality (Figure 5.5).



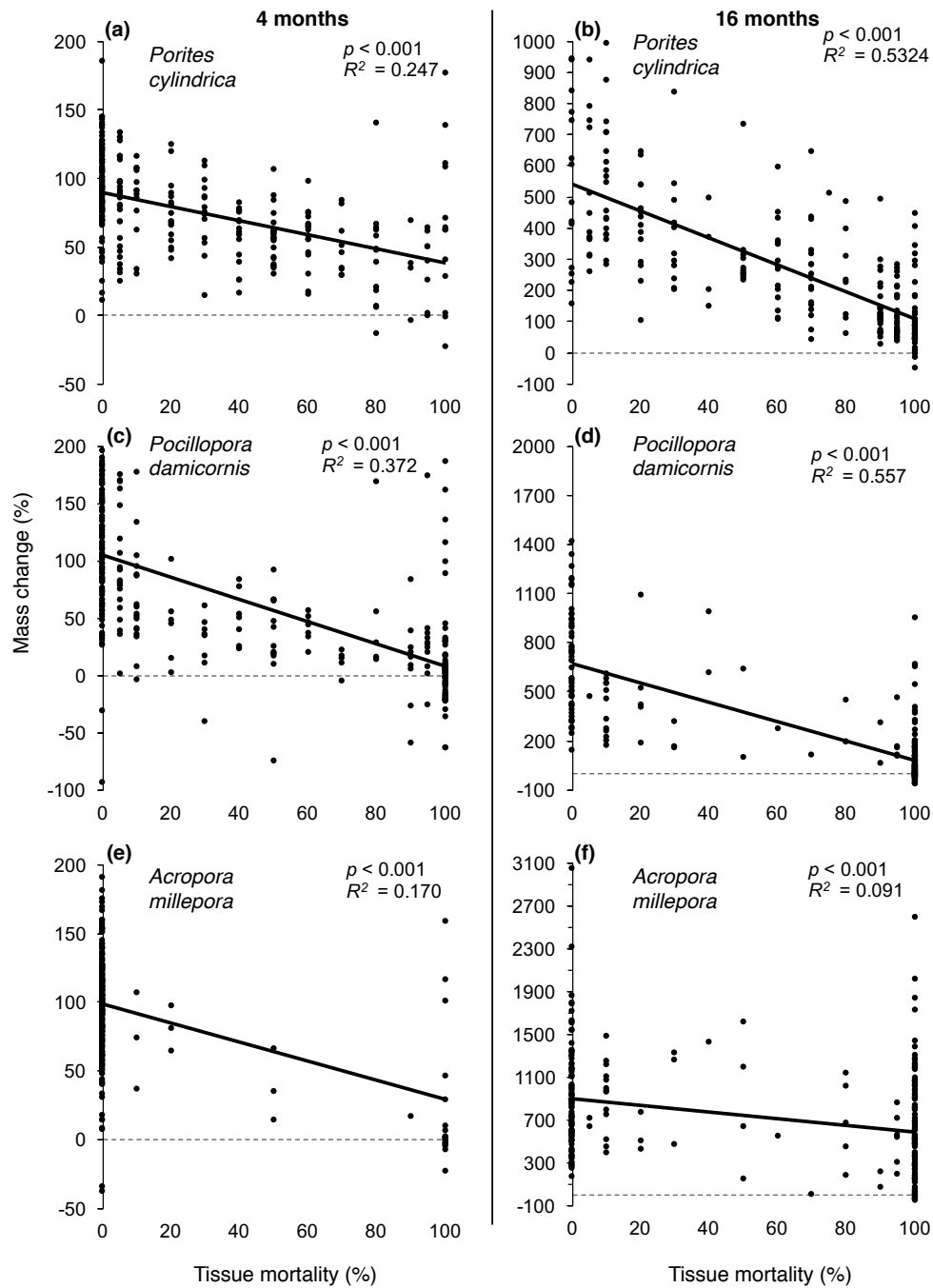


Figure 5.5: Relationship between change in mass (%) and tissue mortality (%) of individual *Porites cylindrica* (a, b), *Pocillopora damicornis* (c, d), and *Acropora millepora* (e, f) corals at four (a, c, e) and sixteen (b, d, f) months. Coefficients of regression ( $R^2$ ) and  $p$ -values are indicated in each graph.

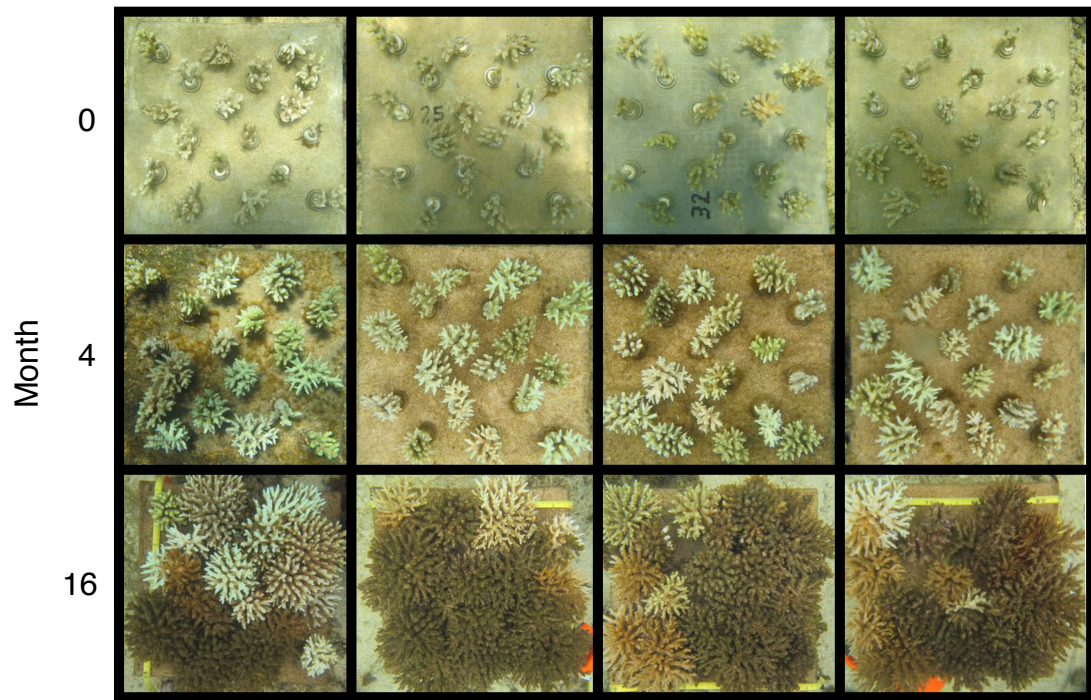


Figure 5.6: *Acropora millepora* monoculture plots at zero (top), four (middle), and sixteen (bottom) months. Corals experienced considerable mortality following a bleaching event that occurred during February 2016.

Mechanisms contributing to lower *P. cylindrica* and *P. damicornis* tissue mortality in polyculture than monocultures are unknown, but may involve reduced corallivory and disease transmission in more diverse plots (Raymundo et al. 2009, Ostfeld and Keesing 2012). The latter seems more likely because corallivorous snails feeding on *P. damicornis* (*Drupella* spp.), *A. millepora* (*Drupella* spp.) and *P. cylindrica* (*Coralliophila violacea*) at sixteen months were uncommon (0-0.22 snails coral<sup>-1</sup>), highly variable across plots, and predator densities did not differ significantly between conspecifics in monocultures and polyculture (Figure 5.7). Greater mortality in monocultures might be expected if diseases were transmitted via coral-to-coral contact (Aeby et al. 2011) or via water- or vector-mediated pathways (Gignoux-Wolfsohn et al. 2012). Disease spread may be hindered by diversity-mediated dilution effects (Johnson et al. 2015). Analogous dilution effects have been documented in other ecosystems (Ostfeld and Keesing 2012), and correlative analyses suggest that coral disease is less prevalent in geographic regions with greater coral diversity (Aeby et al. 2011). Other studies have also found that corals surrounded by heterospecifics experience reduced predation by corallivores implicated in the spread of coral pathogens (Kayal et al. 2011, Johnston and Miller 2014). Future experiments with increased temporal resolution may help identify the biodiversity-mediated mechanisms involved in the patterns we documented.

If the biodiversity effects we document for these three common corals are typical, then reef recovery following major disturbances (e.g. bleaching, *Acanthaster* spp. outbreaks, etc.) depends not only on coral recruitment and growth, but also on the remaining diversity of other corals and how they interact to create synergies that enhance growth and survivorship while suppressing damaging competitors (Shaver and Silliman

2017). As coral diversity declines on modern reefs, they may experience a diversity-meltdown where critical positive interactions are lost and the system fails to recover. It is possible that this may have played a role in the larger losses of corals in the low-diversity Caribbean versus the higher diversity tropical Pacific.

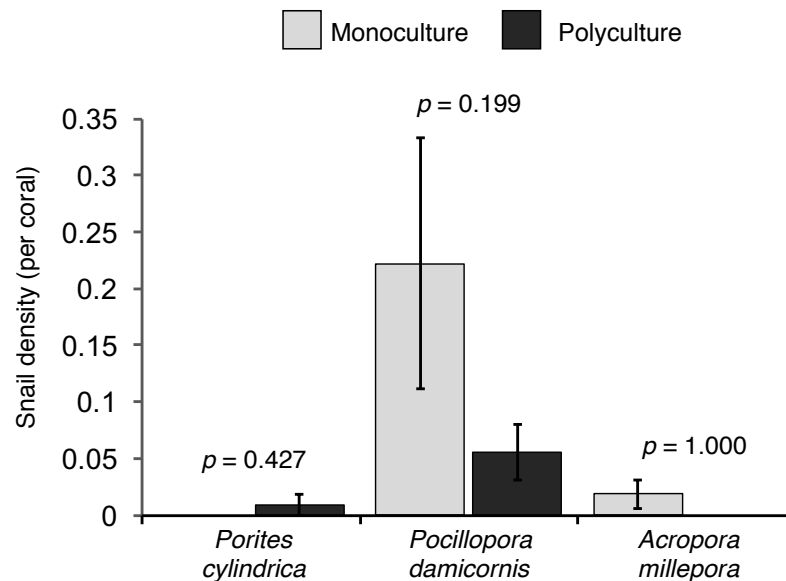


Figure 5.7: Densities of corallivorous snails (*Drupella* spp. and *Coralliophila violacea*) at sixteen months for *Porites cylindrica*, *Pocillopora damicornis*, and *Acropora millepora* in monocultures vs. polycultures. P-values indicate comparisons analyzed with ANOVA using a permutation approach (5000 permutations) in the R (v. 3.3.2) package lmerPerm (v. 2.1.0).

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